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Article *in* River Research and Applications · October 2012

DOI: 10.1002/rra.1513

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RIVER RESEARCH AND APPLICATIONS

River Res. Applic. **28**: 1217–1229 (2012)

Published online 7 April 2011 in Wiley Online Library
(wileyonlinelibrary.com) DOI: 10.1002/rra.1513

USING AN EXPERIMENTAL *IN SITU* FISHWAY TO PROVIDE KEY DESIGN CRITERIA FOR LATERAL FISH PASSAGE IN TROPICAL RIVERS: A CASE STUDY FROM THE MEKONG RIVER, CENTRAL LAO PDR

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ABSTRACT

Fish passage through an experimental vertical-slot fishway was assessed at a floodplain regulator on the Mekong River in Central Laos between April and July 2009. Experiments were conducted to investigate the influence of fishway floor slope (1v:15h or 1v:7.5h) on fish passage success with a view to developing a series of optimal design criteria for the construction of vertical-slot fishways at other barriers to fish passage in the Lower Mekong Basin. A total of 14 661 fish from 73 species were captured during the experiments. Catches were dominated by riverine (white) ($n = 51$; 69% of total) and floodplain (black) species ($n = 15$; 20%) which represented 19 families in total. The work demonstrated that fish were actively attempting upstream passage from the Mekong River to an adjacent floodplain and displayed strong migratory behaviour during river level rises. Migratory activity was greatest during sharp rises in water level but reduced substantially when river level fell. Fish community composition varied greatly among the two fishway floor slopes and the control group. More fish species were collected from control samples, but the most fish and species were collected when the fishway was configured on a moderate hydraulic slope (1v:15h). A range of size classes were also collected from control and moderate-slope groups, but steeper-gradient catches were dominated by larger fish. This study demonstrated that vertical-slot fishways could provide passage for a biodiverse fish community where fish move laterally onto floodplains. The construction of fishways which consider the local fish ecology and hydrology may therefore represent a valuable management tool to help restore important movement pathways for tropical freshwater fish. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS: vertical-slot fishway; migration; Mekong River; fish passage; tropical river

Received 5 July 2010; Revised 30 January 2011; Accepted 11 February 2011

INTRODUCTION

Floodplains are important ecological assets, accounting for much of the natural production in large river systems (Bayley, 1995). Virtually all floodplain ecosystems require regular flooding to maintain connectivity with main river channels in order to release nutrients and provide animals access to new habitats (Junk *et al.*, 1989). Floodplain soils are extremely fertile, and high nutrient loads favour agricultural development (Bayley, 1995). Regular flooding, however, decreases the agricultural productivity of the floodplain because it is difficult to permanently crop areas that are frequently inundated (Sparks, 1995; Islam and Braden, 2006). This paradox has necessitated the development of engineering solutions such as levee banks, regulators and sluice gates to control floodplain inundation events. These engineering structures either reduce or eliminate natural floodplain functions, and productivity quickly decreases, particularly in areas of intensive development (De Graaf, 2003; Thoms, 2003). Reductions in productivity and accessibility have facilitated the decline of floodplain fauna in many rivers throughout the world (Kingsford, 2000).

The Mekong is one of the world's major catchment systems. It drains a total area of 795 000 km^2, is over 4000 km in length and supports over 60 million people. Freshwater fisheries are immensely important throughout the lower Mekong basin, providing on average 48% (Lao PDR) and 79% (Cambodia) of the animal protein intake (Hortle, 2007). More than 80% of rural households in the Mekong basin in Thailand, Lao and Cambodia are involved in a capture fishery which has a first-sale value of between US$2000 and 4000 million per year (Hortle, 2007). The annual yield from the capture fishery in the

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lower Mekong Basin is about two million tonnes, which is approximately 2% of the total world marine and freshwater catch. Whereas the development of floodplain ecosystems has had a worldwide impact on fisheries production, detrimental impacts on the Mekong River are becoming increasingly apparent (Hortle and Suntornratana, 2008).

The Mekong River has an extensive floodplain system extending from the lowland reaches of Lao PDR and Thailand through large and complex wetland systems in Vietnam and especially Cambodia (Kummu *et al.*, 2005). The Mekong floodplains are among the most productive in the world, but a lack of ecological understanding precludes effective management of the system (Campbell, 2005). Fish of the Mekong floodplains are adapted to high natural mortality through early sexual maturation and high fecundity (Lowe-McConnell, 1987). These adaptations provide resilience to fishing exploitation, provided floods of adequate duration and magnitude frequently inundate floodplain habitat and help to maintain productivity (Bayley, 1995). Construction of dams in the upper Mekong however is beginning to reduce incidences of flooding in downstream reaches, and inundation events are declining in frequency (Lu and Siew, 2006). Further development of floodplain systems, with agricultural infrastructure, is also reducing lateral connectivity in many areas (Valbo-Jorgensen and Poulsen, 2000; Nguyen and De Silva, 2006). Continued development of these important ecosystems requires the development of effective mitigation techniques that can restore lateral connectivity with the main river channel to help maintain fisheries productivity.

In large rivers, most fish passage rehabilitation efforts for migratory fish are focused on developing fishways for main channel barriers to longitudinal connectivity (Clay, 1995; Odeh, 1999; Stuart *et al.*, 2007). Fish passage can be less relevant in large biodiverse rivers with high barriers (>12 m) where large-scale habitat changes, reductions in flow regimes and water quality issues often have a much greater impact than reduced connectivity (Pelicice and Agostinho, 2008). Whereas mitigating the impacts of large barriers can prove difficult, fishways have been an effective management tool for providing fish passage at smaller structures (<6 m) (Barrett and Mallen-Cooper, 2006; Baumgartner and Harris, 2007; Mallen-Cooper and Brand, 2007). In some cases, fishways can provide passage for high numbers and biomasses of fish over relatively short periods (Kowarsky and Ross, 1981; Schwalme and Mackay, 1985; Mallen-Cooper, 1996; Stuart and Mallen-Cooper, 1999; Schmetterling *et al.*, 2002; King and Torre, 2007; Stuart *et al.*, 2008a, 2008b; Roscoe and Hinch, 2010). Importantly, to optimize the engineering specifications for a fishway, there needs to be a clear *a priori* understanding of the local hydrology, fish species and size composition and well-defined ecological objectives.

Success of tropical fishways, particularly at large barriers to longitudinal migration, is usually determined from post-construction assessments of effectiveness using trapping or other techniques (Agostinho *et al.*, 2007). Often, this can lead to inappropriate generic conclusions about fishway success especially if swimming ability of local non-salmonid species is not considered during the design and construction phase (Godinho and Kynard, 2009). It is necessary to understand the swimming ability and migratory behaviour of target species before fishways are designed. The design process can then ensure that suitable internal hydraulics exist over a range of hydrological regimes, barrier heights and migratory biomass expected at sites of interest. Many studies gain this knowledge through the use of flume or laboratory trials (Mallen-Cooper, 1992; Castro-Santos, 2004; Haro *et al.*, 2004). These studies are effective because the experimenter has control over hydraulic variables. These types of studies can have reduced scope because work is limited to a small number of target species under limited motivation to migrate under laboratory conditions (Mallen-Cooper, 1999). Providing passage for diverse fish communities, as in tropical systems, introduces a degree of logistical complexity where it is difficult to replicate a range of migratory biomasses and migration strategies in a controlled environment. Under these circumstances, *in situ* field experiments are more appropriate as the experimenter is working with fish that are motivated to migrate under natural conditions.

Several fishways have been constructed in the Lower Mekong Basin, but none demonstrate evidence of a design that integrates information concerning the swimming ability of the target fish species and the local river hydrology (Sripatrptasite, 2005). Most existing floodplain barriers or 'regulators' in tributary systems of the lower Mekong are low level (<6 m) and block important longitudinal migrations along rivers and lateral movements onto floodplain habitats. The broad division of 'black' (floodplain) and 'white' (river channel) fishes in tropical rivers also suggests that lateral fish passage onto floodplains is likely to require different design criteria compared with that in river channel sites. Fishways have been developed for non-salmonids that have passed up to 26 species (Travade *et al.*, 1998; Mallen-Cooper, 1999; Stuart and Mallen-Cooper, 1999). Whereas this species diversity may be satisfactory in many temperate rivers, it represents a small fraction of the estimated 2000 species present in the Mekong River (Van Zalinge *et al.*, 2004). Common fish passage options for lateral movements include pool-type, nature-like and Denil fishways. The most appropriate fishway for the Mekong floodplain situation is the vertical-slot design because it can operate over wide headwater (floodplain) levels, is known to pass a wide range of species and copes with relatively high biomass (Rodríguez *et al.*, 2006).

DOI: 10.1002/rra

The present study sought to determine the suitability of a vertical-slot fishway to provide lateral fish passage for fish attempting to access floodplain habitats from the Mekong River. A series of *in situ* experiments were undertaken at a barrier where fish were attempting to access a major floodplain. Experimental manipulations of flow and turbulence were used to determine the optimal design criteria to guide potential application at other sites in the Lower Mekong Basin.

METHODS

Study site

The study was conducted at a floodplain regulator adjacent to the Mekong River at Pak Peung village (Bolikhamxay Province) in central Lao PDR (Figure 1). The concrete regulator was constructed (in the 1960s) to prevent inundation of extensive floodplain rice crops during increases in Mekong River level during the wet season. The regulator is 10 m high and contains three manually operated sluice gates which release water from an upstream wetland. Each gate is capable of delivering a maximum of 80 Ml day^{-1} (0.93 m^3 s^{-1}). Gates are initially operated to drain the floodplain wetland to prevent crop damage following high-rain events early in the wet season. The gates are adjusted daily and during this period, and fish might move 180 m downstream (from the floodplain to the river) through the sluice gates, but upstream passage (from the river to the floodplain) is completely blocked. The gates are closed during high Mekong River levels to prevent further crop damage from water entering the wetland (usually later in the wet season). Under these conditions, the regulator is a barrier to both upstream and downstream fish movements.

Experimental fishway

A vertical-slot fishway, constructed out of reinforced mild steel (1.5 mm diameter), was installed parallel with the left-hand (looking downstream) training wall downstream of the regulator and secured in place with a combination of sandbags and high-tensile cable. A block and tackle with an endless chain was fitted to an overhead gantry and used to manipulate the height of the fishway in response to rising water levels. A sandbag wall was erected upstream of the structure to direct flow from the regulator through the experimental unit. The fishway unit comprised four pools which were 1500 mm × 1000 mm in size. Larger pool sizes were considered, but accommodating a larger pool size would require larger amounts of water, which would increase the overall weight of the experimental unit. It was also hypothesized that mostly small-bodied black species, and sub-adult white species, would attempt to access floodplain habitat, so a smaller pool size was selected for initial experiments. The vertical slots were 1400 mm high with a slot width of 150 mm.

Figure 1. Photo of the Pak Peung floodplain regulator, demonstrating the location and size of the experimental fishway. The trap beside the fishway is sampling fish for the non-fishway control trial at the upstream limit of migration. The Mekong River is approximately 180 m downstream of the study site.

DOI: 10.1002/rra

Experimental design

To compare fish communities attempting to ascend the fishway (control) with fish successfully ascending (treatments), fish were collected from two locations within the fishway over a period of 44 days in the early wet season between April and July 2009. Treatments involved establishing the fishway on two hydraulic gradients and assumed a Cd of 0.7. The treatments were a moderate gradient (1v:15h or 6%; max velocity $1.4\,\mathrm{m\,s^{-1}}$, average turbulence $96\,\mathrm{W\,m^{-3}}$) and a steep gradient (1v:7.5h or 12%; max velocity $1.98\,\mathrm{m\,s^{-1}}$, average turbulence $271\,\mathrm{W\,m^{-3}}$). More conservative slope gradients were considered in a brief pilot study in 2008, but anything less than the two gradients described here were considered to provide inadequate attraction for migrating fish. Steeper gradients with higher discharge were subsequently adopted.

Once the desired hydraulic conditions were achieved in each treatment, fish passage was assessed by placing a fish trap (1500 mm × 1000 mm × 1400 mm; 4-mm mesh) upstream of the top baffle. The experiment also included a non-fishway control, where migrating fish were collected from outside the experimental unit. The control sought to quantify the number of fish attempting to migrate at the site and provided a basis for comparison with treatment replicates. This sought to determine the structure of the migratory fish community that did not enter the fishway. Control sampling began by releasing water adjacent to the fishway to provide an attraction flow to a trap that was established next to the fishway at the upstream limit of migration, and any migrating fish were collected. All fish captured were identified, counted, measured and released upstream at the completion of experiments.

Each control and treatment replicate ran for 2 h after which the trap was retrieved and any fish identified, measured (total length) and weighed. Replicates were completed each day between 0700 and 1500 h. It was unknown whether the structure of migratory fish communities would vary with time of day. To control for this potential effect, the fishway was assessed using a randomized block design where one ‘block’ was completed every 3 days. Experimental treatments and the control were subsequently assigned to one of three potential periods each day (morning: 0700–1000 h, midday: 1100–1300 h, afternoon: 1400–1700 h). The three replicates (control and two treatments) were completed per day, but 3 days were required to complete all time of day and treatment combinations. A total of six full blocks were completed over the study period. No night sampling was undertaken.

Data analyses

Data were analysed using S-PLUS (TIBCO Software Inc., Palo Alto, CA) and PRIMER V6.0 (PRIMER-E Ltd, Ivybridge, UK). Differences in length distributions of fish collected from control and treatment samples were compared using a Kolmogorov–Smirnov (KS) pairwise comparison. This test computes a test statistic (ks) that is based on the largest difference between two cumulative length frequency distributions. The length frequency data of all fish species were then pooled to construct length frequency histograms for each treatment and control.

Differences in fish community structure among experimental blocks, fishway slope and time of day were investigated using permutational analysis of variance (PERMANOVA). All tests were based on square-root-transformed data using Bray–Curtis similarities (with 999 permutations). ‘Block’ and floor slope were treated as fixed factors, but time of day was random. It was largely unknown at the commencement of the study whether different species migrated at different times of the day. This was identified as a factor which could potentially confound experimental results if slope experiments were conducted in different diurnal periods. Preliminary analysis identified no differences that could be attributed to time of day in fish community structure, so it was removed as a factor from subsequent analysis to permit further exploration of the effect of floor slope and experimental blocks. Two-way analysis of similarities was subsequently used to determine whether the fish communities differed among experimental groups (treatment and controls) or among daily experimental blocks. This test sought to identify both the effect of fishway slope and also any natural change in fish communities as time progressed through the experiment. In all analysis of similarities tests, 999 Monte Carlo randomizations were used to calculate approximate probabilities and global R-values. Sample differences were plotted using non-metric multi-dimensional scaling ordinations to visually represent any group differences.

RESULTS

General catch information

Fish were extremely motivated to migrate, jumping at the base of the regulator and attempting to ascend shallow flowing water on the concrete apron. In total, 14 661 fish from 73 species were captured during the experiments (Table I). Catches were dominated by riverine (white) species ($n = 51$; 69% of total), but several floodplain (black) species were also recorded ($n = 15$; 20%). Species represented 19 families in total, but 96% of the catch represented only five families (Cyprinidae = 69%; Ambassidae = 22%, Belonidae = 4%; Clupeidae = 1%; Mastacembelidae = 1%), and 34 species comprised less than 10 individuals (Table I). Three species, *Parambassis siamensis* (black, $n = 3277$), *Barbonymus gonionotus* (white, $n = 3206$) and *Rasbora*

DOI: 10.1002/rra

Table I. Total number of fish caught from the Mekong floodplain experimental fishway unit over the study period. Numbers refer to all species pooled across blocks for all experimental controls and treatments performed

Species name	Family	Control	1:15	1:7.5	Grand total
White species					
Parambassis siamensis	Ambassidae	819	1948	510	3277
Barbonymus gonionotus	Cyprinidae	160	1552	1494	3206
Barbonymus schwanenfeldii	Cyprinidae	0	651	9	660
Hampala dispar	Cyprinidae	277	249	56	582
Xenentodon canciloides	Belonidae	406	136	17	559
Paralaubuca typus	Cyprinidae	62	262	24	348
Osteochilus lini	Cyprinidae	4	149	144	297
Amblypharyngodon chulabhornae	Cyprinidae	179	11	0	190
Clupeichthys aesiamnesis	Clupeidae	155	0	0	155
Osteochilus schlegelii	Cyprinidae	0	8	86	94
Henicorhynchus ornatipinnis	Cyprinidae	2	57	34	93
Puntius partipentazona	Cyprinidae	33	2	34	69
Raiamas guttatus	Cyprinidae	2	37	28	67
Epalzeorhynchos frenatum	Cyprinidae	0	0	54	54
Hampala macrolepidota	Cyprinidae	22	25	1	48
Macrognathus semiocellatus	Mastacembelidae	46	0	0	46
Badis ruber	Badidae	31	10	0	41
Puntius orphoides	Cyprinidae	1	20	18	39
Osteochilus hasselti	Cyprinidae	2	11	22	35
Probarbus jullieni	Cyprinidae	4	22	8	34
Cephalocassis borneensis	Ariidae	0	32	2	34
Henicorhynchus siamensis	Cyprinidae	27	3	2	32
Sinibrama melrosei	Cyprinidae	0	25	2	27
Mastacembelus armatus	Mastacembelidae	15	0	1	16
Scaphognathops stejnegeri	Cyprinidae	2	4	10	16
Labiobarbus siamensis	Cyprinidae	0	5	11	16
Macrognathus siamensis	Mastacembelidae	15	0	0	15
Puntius jacobusboehlkei	Cyprinidae	0	0	10	10
Puntius brevis	Cyprinidae	1	9	0	10
Cyclocheilichthys armatus	Cyprinidae	0	2	6	8
Barbicthys laevis	Cyprinidae	1	4	2	7
Acanthopsoides delphax	Cobitinae	4	0	1	5
Hypsibarbus vernayi	Cyprinidae	1	2	2	5
Pristolepis fasciata	Nandidae	1	2	1	4
Amblyrhynchichthys truncatus	Cyprinidae	0	2	2	4
Hemibarbus labeo	Cyprinidae	1	2	1	4
Scaphognathops spp.	Cyprinidae	1	2	1	4
Cyclocheilichthys repasson	Cyprinidae	0	1	2	3
Cyclocheilichthys apogon	Cyprinidae	0	0	3	3
Thynnichtys thynnoides	Cyprinidae	0	0	3	3
Brachygobius mekongensis	Gobionellinae	2	0	0	2
Chitala ornata	Notopteridae	0	2	0	2
Barbonymus altus	Cyprinidae	0	2	0	2
Mystus mysticetus	Bagridae	1	0	1	2
Cyprinus carpio	Cyprinidae	0	1	1	2
Notopterus notopterus	Notopteridae	0	0	2	2
Labiobarbus leptocheilus	Cyprinidae	1	0	0	1
Squalidus atromaculatus	Cyprinidae	1	0	0	1
Hypophthalmichthys molitrix	Cyprinidae	0	0	1	1
Acrossocheilus iridescens	Cyprinidae	1	0	0	1
Tetraodon cambodgiensis	Tetraodontidae	0	1	0	1
Total white species	–	2280	5251	2606	10 137
Black species					
Rasbora dusonensis	Cyprinidae	1	1567	1057	2625
Rasbora rubrodorsalis	Cyprinidae	252	248	81	581
Rasbora daniconius	Cyprinidae	28	303	169	500

(*Continues*)

DOI: 10.1002/rra

Table I. (Continued)

Species name	Family	Control	1:15	1:7.5	Grand total
Esomus metallicus	Cyprinidae	10	181	2	193
Esomus longimanus	Cyprinidae	28	73	0	101
Rasbora trilineata	Cyprinidae	32	1	0	33
Rasbora pauciperforata	Cyprinidae	0	21	7	28
Nemacheilus platiceps	Nemacheilinae	12	0	2	14
Rasbora aurotaenia	Cyprinidae	0	0	9	9
Oreochromis niloticus	Cichlidae	3	1	0	4
Acantopsis spp.	Cobitidae	4	0	0	4
Anabas testudineus	Anabantidae	3	0	0	3
Trichogaster microlepis	Osphronemidae	3	0	0	3
Nandus oxyrhynchus	Nandidae	1	0	0	1
Yasuhikotakia longidorsalis	Botiinae	0	1	0	1
Total black species	–	377	2396	1327	4100
Unknown species					
Unknown 3	–	320	0	0	320
Unknown 2	–	2	15	72	89
Unknown 6	–	1	4	2	7
Unknown 7	–	3	0	0	3
Unknown 1	–	1	0	2	3
Unknown 4	–	1	0	0	1
Unknown 8	–	1	0	0	1
Total unknown species	–	329	19	76	424

dusonensis (black, $n = 2625$), comprised 62% of total catch. Eight species were unable to be indentified and are presently undergoing more detailed taxonomic classification. Twenty-two of the 73 species were only collected within the fishway three times throughout the experiment. Of the remaining 51 species, 47 were recorded using the fishway.

Influence of fishway slope

The most number of fish collected were during moderate-slope treatments ($n = 7666$), but more species ($n = 52$) were collected from control samples (Table I). Species appeared to fall within three main groupings based on passage success within the experimental unit. Firstly, there were species which only migrated when the fishway was established on a steep slope. These species ($n = 20$) were either absent or collected in relatively low abundance during control and moderate-slope treatments. Another group of fish were collected only from control groups ($n = 14$) and were absent from treatments. The final group of fish ($n = 39$) were collected from both control and treatment groups irrespective of fishway slope.

A three-factor analysis (based on the randomized block design) identified significant differences among blocks (PERMANOVA; Table II), which arose from a progressive change in migratory fish community from the beginning to the end of the study period. Many fish were migrating at the commencement of experiments, but the numbers gradually decreased with time. Differences in fish community composition were also detected among different floor slopes (PERMANOVA; Table III) because of changes in relative abundances of several species among experimental treatments. This was largely due to the high number of individuals collected from the moderate-slope group overall and the absence of several species from control samples. For instance, *Parambassis siamensis*, *Rasbora rubrodorsalis* and *Xenentodon cancila* were collected in significantly higher abundances from control samples than from either treatment sample. In contrast, several species such as *Barbonymus gonionotus*, *Rasbora dusonensis* and *Osteochilus lini* were more frequently collected from the two treatment groups rather than from the control. These differences in fish community composition provided separation of treatment groups in ordinal space (Figure 2). No significant differences

Table II. PERMANOVA results for differences in fish community structure among factors assessed during the experimental study

Effect	*df*	SS	MS	PS-F	*p*
Among blocks	5	25 498	5099	1.77	0.015
Slopes (blocks)	12	24 502	2041	1.94	0.001
Time of day (blocks)	12	12 911	1075	1.03	0.416
Blocks × slope × time of day	14	14 496	1035	1.07	0.404

df, degrees of freedom; SS, sum of squares; MS, mean squares; PS-F, pseudo-*F* value; *p*, probability based on multiple permutations of the data.

DOI: 10.1002/rra

Table III. Length statistics for species captured within the experimental fishway facility. For brevity, only species with 10 or more individuals have been included

Species name	Family	*n*	Mean ± SD	Min	Max
Amblypharyngodon chulabhornae	Cyprinidae	94	34 ± 7	20	75
Badis ruber	Badidae	31	35 ± 5	25	45
Barbonymus gonionotus	Cyprinidae	643	61 ± 16	29	116
Barbonymus schwanenfeldii	Cyprinidae	36	45 ± 10	31	80
Cephalocassis borneensis	Ariidae	11	95 ± 9	85	106
Clupeichthys aesiamnesis	Clupeidae	25	37 ± 4	30	45
Esomus longimanus	Cyprinidae	72	54 ± 9	40	80
Esomus metallicus	Cyprinidae	92	53 ± 9	34	75
Epalzeorhynchos frenatum	Cyprinidae	11	54 ± 9	35	72
Hampala dispar	Cyprinidae	358	44 ± 11	25	127
Hampala macrolepidota	Cyprinidae	48	38 ± 9	25	75
Henicorhynchus ornatipinnis	Cyprinidae	93	67 ± 12	35	115
Henicorhynchus siamensis	Cyprinidae	30	36 ± 25	20	125
Labiobarbus siamensis	Cyprinidae	14	91 ± 12	70	111
Macrognathus semiocellatus	Mastacembelidae	46	138 ± 20	100	176
Macrognathus siamensis	Mastacembelidae	15	145 ± 34	42	191
Mastacembelus armatus	Mastacembelidae	16	130 ± 37	65	200
Nemacheilus platiceps	Nemacheilinae	14	48 ± 13	33	78
Osteochilus hasselti	Cyprinidae	32	127 ± 25	95	195
Osteochilus lini	Cyprinidae	201	105 ± 17	19	145
Osteochilus schlegelii	Cyprinidae	51	106 ± 10	81	134
Paralaubuca typus	Cyprinidae	235	50 ± 7	29	87
Parambassis siamensis	Ambassidae	945	46 ± 8	24	92
Probarbus jullieni	Cyprinidae	36	69 ± 9	50	84
Puntius jacobusboehlkei	Cyprinidae	10	155 ± 24	132	195
Puntius orphoides	Cyprinidae	39	56 ± 7	45	85
Puntius partipentazona	Cyprinidae	20	34 ± 3	28	41
Raiamas guttatus	Cyprinidae	69	61 ± 12	42	111
Rasbora aurotaenia	Cyprinidae	25	79 ± 7	64	90
Rasbora daniconius	Cyprinidae	412	60 ± 10	22	96
Rasbora dusonensis	Cyprinidae	618	76 ± 10	24	105
Rasbora rubrodorsalis	Cyprinidae	351	36 ± 9	21	79
Scaphognathops stejnegeri	Cyprinidae	17	46 ± 6	35	62
Sinibrama melrosei	Cyprinidae	46	43 ± 9	35	81
Xenentodon canciloides	Belonidae	452	158 ± 40	20	285
Unknown 3	–	37	56 ± 7	45	79
Unknown 2	–	25	45 ± 6	30	57

n, the total number of fish measured; mean ± SD, the mean of all measured fish and one standard error; Min, the smallest fish measured; Max, the largest fish measured.

among different diurnal periods indicated that the structure of the migratory fish community did not vary during daylight hours (PERMANOVA; Table II).

Effect of river flow on fishway use

Daily mean fish passage was relatively high early in the study but decreased substantially during the final stages (Figure 3). The commencement of the study period coincided with a sharp increase in tailwater water levels dictated by Mekong River levels (from 2.39 to 4.40 m) following substantial wet season rainfall events in upstream tributary catchments. Tailwater levels eventually peaked, and the total number of fish species and individuals thereafter collected substantially declined from both treatment and control samples. A correlation between river level and total fish migration numbers identified a poor relationship ($R = 0.09$) because most increases in fish migration occurred during the initial level rise, suggesting that change in water level may be a more meaningful factor (Figure 3). Migration rates were subsequently plotted against change in daily level, and a much stronger correlation was observed ($R = 0.53$; Figure 4). These observations provide preliminary evidence that migration rates and changing hydrograph could be inherently linked,

DOI: 10.1002/rra

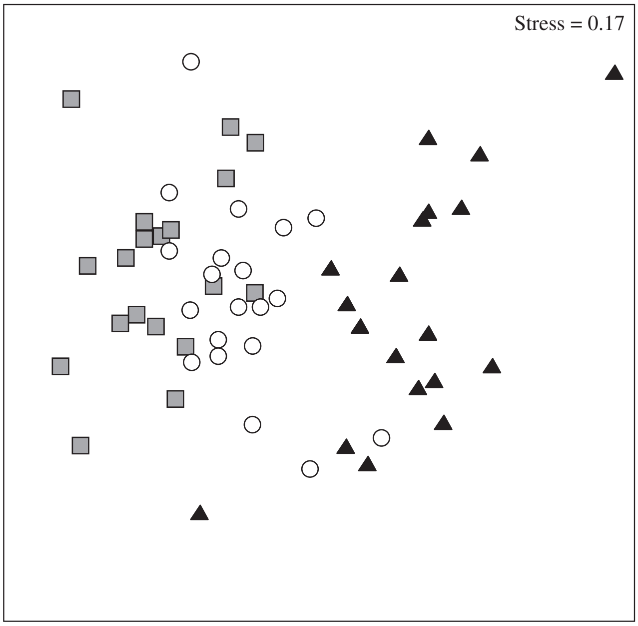

Figure 2. Multi-dimensional scaling ordination of fish communities captured during control (black triangle), 1:15 (white circle) and 1:7.5 (grey square) treatments assessed during this study.

but the relationship was not consistent across species. *Xenentodon canciloides* continued to use the experimental fishway during a falling hydrograph whereas *Rasbora dusonensis*, *Barbonymus gonionotus*, *Osteochilus lini*, *Cyclocheilichthys armatus* and *Rasbora daniconius* were only collected during a rising hydrograph. These species were notably absent whenever levels in the Mekong were falling.

Size class differences. Most of the fish collected were from a small to moderate size range, 19–285 mm long, but the greatest proportion of fish were relatively small, <100 mm long (Table III). Fish collected from the control group were significantly smaller than fish collected from either of the two treatment groups (KS: $ks_{ctrl\ vs\ 1:15} = 0.240$, $p < 0.001$; $ks_{ctrl\ vs\ 1:7.5} = 0.415$, $p < 0.001$). *Clupeichthys aesiamnesis*, *Amblypharyngodon chulabhornae* and *Eosomis* spp. were almost virtually absent from catches during steep-slope (1v:7.5h) experiments, and no fish less than 40 mm long were able to ascend steep floor slopes (Figure 5). Changes in the catch of fish less than 100 mm long contributed to significant differences between both treatment groups (KS: $ks_{1:15\ vs\ 1:7.5} = 0.182$; $p < 0.001$). In contrast, catches of

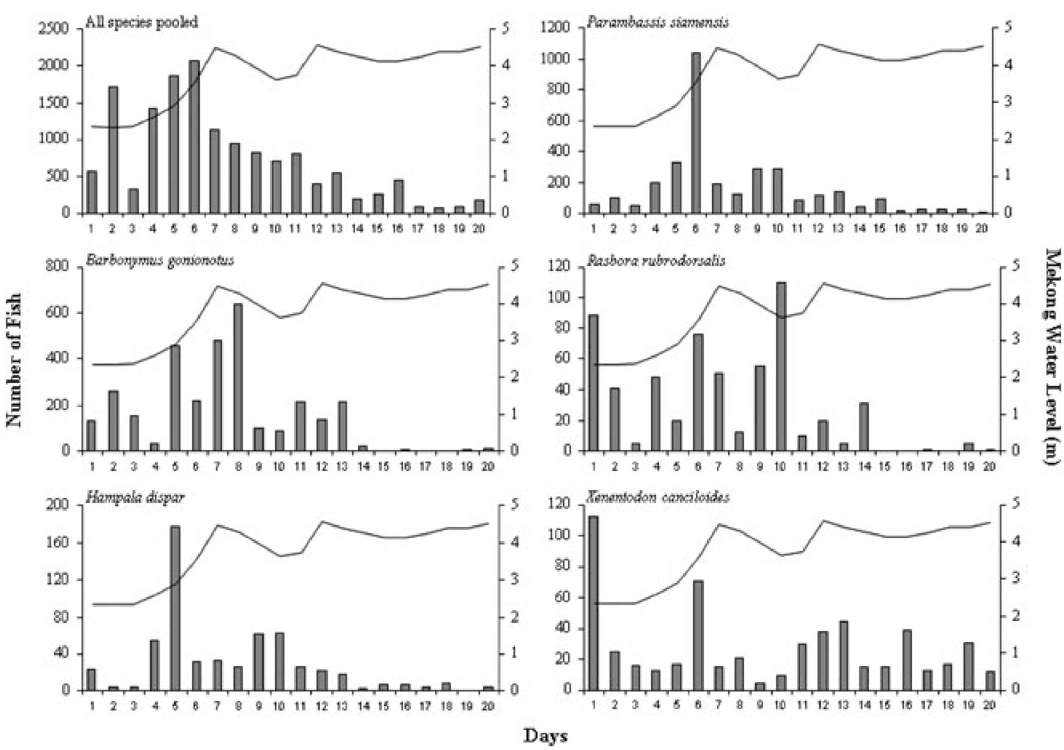

Figure 3. Relationship between daily fish catches and Mekong River level over the study period. Graphs represent the longest period where trapping was undertaken on consecutive days. Data are presented for all species pooled and five of the most abundant species collected.

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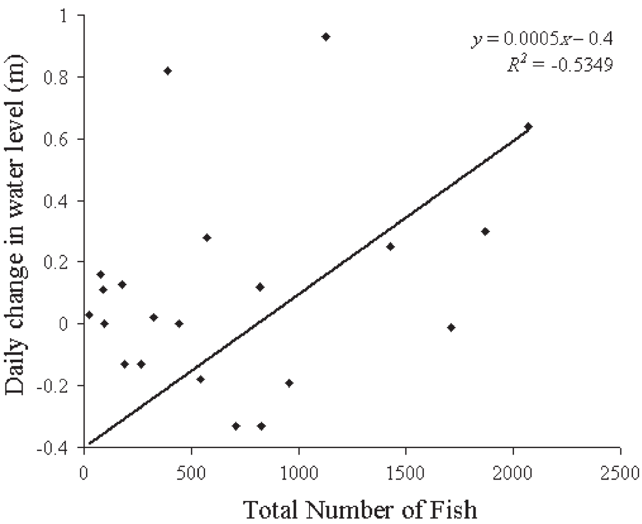

Figure 4. Scatterplot of the relationship between change in water level and migratory fish movements.

larger fish were higher for the steeper slope. Some species, including *Rasbora dusonensis*, *Barbonymus schwanenfeldii*, *Rasbora daniconius* and *Osteochilus lini*, were poorly represented from control samples but were more abundant when slope increased. Substantially more fish (80–120 mm long) were collected on a moderate slope (1v:15h) whereas a greater proportion of fish (120–160 mm long) were collected during steep-slope trials.

DISCUSSION

Fishways in large tropical systems have frequently performed very poorly, not passing all migratory species, specific life stages or only a small fraction of the migratory biomass (Pelicice and Agostinho, 2008). Many existing tropical fishways have also been studied post-construction, which can provide little opportunity to advise the construction of future fishways especially if the structure is deemed unsuccessful (Agostinho *et al.*, 2007; Godinho and Kynard, 2009). Four steps in developing fishways for non-salmonid fishes have been suggested (Mallen-Cooper, 1999): (i) identify the migratory fish community; (ii) test fish in an experimental fishway; (iii) design and build the fishway; and (iv) assess the fishway. We used a specific control to identify the migratory fish community and chose an *in situ* experimental fishway to gain data from wild migrating fish on the Mekong River. The experimental vertical-slot fishway demonstrated substantial potential for wider application at sites with a diverse tropical fish community.

The use of fishways to facilitate passage in tropical rivers is complicated by high migratory biomass, variable hydrology and higher species richness than in temperate

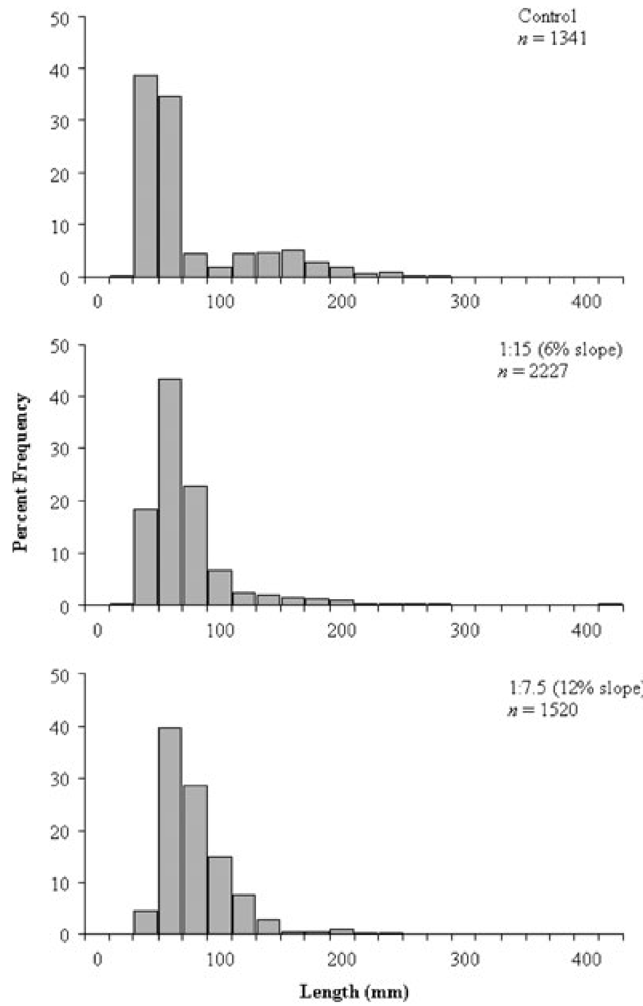

Figure 5. Length distributions of fish collected in each experimental treatment and control. Values are pooled across all species and experimental blocks.

zones (Oldani and Baigún, 2002). Historically, fish passage was only thought important in an upstream direction and confined to the main channel (Godinho and Kynard, 2009). The requirement for fish to access the floodplain was more recently determined for tropical systems in Bangladesh where flood control structures are managed to improve fish passage (Sultana and Thompson, 1997; Larinier and Marmulla, 2004). There are two essential components required to construct an effective fishway. Firstly, it is important to define the migratory fish assemblage and set ecological targets for success. High numbers of species and size classes were actively recorded performing lateral movements from the main channel to the floodplain at the Pak Peung regulator. Secondly, it is important to understand the local hydrology, including how fish respond to changes in hydraulic regime. This information can then be used to

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determine design criteria necessary to maintain optimal fishway operation at different stages of the hydrograph.

This design complexity was highlighted by the identification of three broad responses to the experimental fishway, reflecting a range in swimming ability and behaviour. Fish with stronger swimming abilities readily ascended the experimental unit and were captured in relatively high abundance from the fishway exit. In contrast, fish with poorer swimming abilities were only collected under control conditions. These different responses suggest that whereas the construction of fishways on moderate slopes will provide good passage for most species, a proportion of weaker-swimming fish might still be unable to ascend. In temperate rivers, many species have different lateral migratory requirements, depending on life history stage, flow changes or time of year (Coops *et al.*, 2006). It is likely that similar requirements exist in large tropical systems, which provide a difficult and ongoing challenge to design a single fishway that can provide upstream passage for all migratory species and life stages over a varied hydrograph (Godinho and Kynard, 2009).

Many species of fish were observed to migrate through the experimental fishway, but there were substantial differences in ascent success between control and treatment groups. The control sought to quantify the structure of the migratory fish assemblage, but in some cases, catches were smaller than those in treatment groups. Several possibilities could account for this anomaly. Firstly, the trap was specifically designed to target smaller species. For this study, it was chosen for logistics, and we considered that either black fishes, which are mostly small and medium bodied, or juvenile white fishes would dominate the migratory fish assemblage. Larger fish are known to exhibit trap shyness (Stuart *et al.*, 2008a, 2008b) and were potentially reluctant to enter the trap. Control sampling was also undertaken using a dispersed discharge through the trap, but there were several species that were only collected from steep-gradient treatments with a concentrated discharge through the vertical slot. This suggests that higher-gradient fishways or attraction jets of water could provide more attraction for migrating fish, thus resulting in lower catches from controls.

Species collected during treatment groups supported the use of an *in situ* approach to obtain realistic data on migratory fish assemblages and swimming abilities (Mallen-Cooper, 1999). Most species readily ascended the fishway, suggesting that vertical-slot fishways have excellent potential to rehabilitate lateral migrations in the Mekong River. Moderate slopes suited most species and size classes, but there were some species which were only collected during controls or the steep-slope treatments. Changes in attraction discharge or internal fishway hydraulics may explain some of these observed differences. Some species collected from the control samples appeared to avoid the fishway when slope was increased. Fishways with high flow and turbulence are widely understood to limit the passage of some species (Liu *et al.*, 2006; Tarrade *et al.*, 2008). Under these circumstances, reducing floor slope may be a useful mechanism to increase passage of some species, but the decrease in associated entrance attraction flow would likely inhibit the passage rates of others. In general, the influence of pool turbulence on fish passage is not well understood but appears to be an important factor for small-fish passage in vertical-slot fishways on large tropical and temperate rivers in Australia (Stuart *et al.*, 2008a, 2008b). Recent research work also raised the potential for altering pool turbulence by installing flow-spoiling devices (Wu *et al.*, 1999; Tarrade *et al.*, 2008) or through the addition of sills into the middle of each vertical slot (Mallen-Cooper *et al.*, 2008). Fitting these hydraulic modifiers to the vertical-slot design can substantially increase small-fish passage success and provide an inexpensive mechanism to increase functionality whilst potentially reducing construction costs. Neither option was considered as part of the present study on the Mekong River, but further quantitative work in this area may provide substantial benefits given the differences in fish responses to altered slopes.

An additional solution for fish passage, where strong-swimming and weak-swimming species co-occur, is the construction of multiple fishways. For instance, high-slope fishways with increased attraction would provide an effective passage solution for strong-swimming species (Pon *et al.*, 2009). Construction of an additional fishway with more conservative internal hydraulics might then cater for poorer-swimming species (Stuart *et al.*, 2008a, 2008b). The cumulative benefit of both structures would provide a solution that facilitates the passage of most migratory species at any given site. Cost, however, is a major limiting factor in any fishway construction exercise (Barrett and Mallen-Cooper, 2006), and constructing multiple fishways requires a high capital outlay. In the Lower Mekong Basin, further investigation of these design alternatives would be a sound investment before constructing fishways for floodplain development projects.

Fishways require careful design and knowledge of the local fish ecology and hydrology to be truly effective (Clay, 1995). Performing *in situ* research using an experimental facility provided information on species richness and total fish abundance, which can inform the design of future fishways. A challenge for fisheries managers in the Lower Mekong Basin is to successfully design a vertical-slot fishway that maintains ecological functionality with large fluctuations in river level. Tropical river systems are largely deemed as highly biodiverse and are capable of supporting substantial fish biomass (Winemiller and Jepsen, 1998). Biomass is occasionally considered during fishway design phases but is often poorly defined in tropical systems (Stuart *et al.*, 2007). Most examples in tropical systems refer to

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longitudinal rather than lateral movements. Biomass is important in vertical-slot fishways as it primarily determines the required pool volume and slot width. To fully optimize fishway construction at future floodplain sites, some accurate estimates of migratory biomass would be an essential criterion to help develop ecological fish passage objectives.

The diversity and composition of the downstream fish community provided evidence of floodplain regulators acting as a barrier to lateral migrations between the main river and the floodplain habitat. Temporal changes in fish migration rate further suggested that hydrological changes provide an important cue for fish migration in the Mekong. The large numbers of fish migrating upstream at the floodplain regulator site were actively attempting to access the upstream wetland. There are two broad modes of colonization for tropical floodplain wetlands: active migrations and passive drift (Craig *et al.*, 2004). Most species observed migrating at the Pak Peung regulator were juvenile riverine (white) species attempting to access nursery habitat within the upstream wetland. Tropical fish exhibit fast growth rates in floodplain habitats, and many riverine (white) species are known to access floodplains for growth and development (De Graaf, 2003). Numerous juvenile Jullien's golden carp (*Probarbus jullieni*), a species that has declined significantly throughout the Lower Mekong Basin, were actively collected attempting to access wetland habitat. The disconnection of floodplain habitat has been a major factor in listing this species as endangered on the IUCN red list (Baird, 2006). Furthermore, most production in large rivers occurs during periods of wetland inundation (Copp, 1989). These active migrations can be facilitated either by modifying operating protocols of wetland regulators (Larinier and Marmulla, 2004) or, as we have determined, through the construction of suitable fishways. Passive movements of larval fish were not investigated during our study but are an important component of floodplain colonization for species that spawn in main channel habitats (Craig *et al.*, 2004). Fishways have little capacity to deal with passive drifting phases, so alternative solutions would be required to ensure such species benefit from any wetland rehabilitation works.

Understanding the structure of the migratory community is an important consideration in effective fishway design. There was a substantial diversity in fish movement strategies displayed by the migratory community collected from the Lower Mekong Basin. It is important to understand how and when fish respond to changes in local hydrology to ensure that fishways are designed for optimal operation during peak migration periods. Changes in water level and river flow are widely reported as an important cue for fish to undertake both longitudinal and lateral migrations (Beyers and Carlson, 1993; Gehrke *et al.*, 1999; Humphries *et al.*, 1999; Nilsson *et al.*, 2005). Maintaining optimal fishway operation over a range of hydrological conditions is therefore an important design consideration essential to successfully establishing river–floodplain connectivity in the Lower Mekong Basin. Adult fish communities of the Lower Mekong Basin are highly migratory and known to migrate long distances in response to a rising hydrograph (Poulsen *et al.*, 2002). Many large-bodied species (e.g. >300 mm long, such as *Hemibagrus* spp., *Chitala* spp., *Pangasius* spp.) were notably absent from fishway captures and were also absent from similar investigations undertaken on the Mun River (Sripatprasite, 2005). Surveys of local fishers at Pak Peung suggested that some large-bodied species were in the vicinity of the study site (*Hemibagrus* spp., *Channa* spp., *Chitala* spp. and *Pangasius* spp.). Fish were not harvested in high numbers however, and it was explained that these fish generally move at night and during much higher river levels.

Many large (>1 m long) tropical fish species are not known to use fishways in South America (Godinho and Kynard, 2009). Our experimental unit was specifically designed to cater largely to small-bodied and medium-bodied species. The absence of many large-bodied fish could be attributed to behavioural inhibitions to an experimental fishway that was designed for small fish. Factors such as relatively narrow slot widths (Stuart *et al.*, 2008a, 2008b), reduced fishway depth (O'Brien *et al.*, 1999), changing discharge (Mallen-Cooper and Stuart, 2007) or trap design (Swales, 1981) could have contributed. We chose the smallest application of the vertical-slot design, originally used for small-sized and medium-sized catadromous species (40–500 mm) in eastern Australia (Mallen-Cooper, 1992) because of the logistics of adjusting the slope of the fishway in the field and the assumed composition of the fish assemblage migrating laterally onto the floodplain. In many parts of the Lower Mekong Basin, large species are important both ecologically and as components of commercial and sustenance fisheries (Hogan *et al.*, 2004). These species undertake longitudinal riverine migrations (Poulsen *et al.*, 2002), but the extent and role of lateral movements are unclear. Further work is needed to quantify these aspects for lateral fish passage before directly applying the results of the present study to other barriers. Experimentation, potentially using fishway designs with wider slot widths, increased pool volume and larger trap mesh size would be useful to determine whether fishways can adequately provide passage for large-bodied species and higher biomass.

CONCLUSION

Tropical fishways have often failed because designs that were applied failed to account for swimming ability and behaviour of target species (Mallen-Cooper, 1999). Laboratory-based

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swimming performance trials are a good mechanism to obtain swimming performance data but are often limited to a small number of species. Using wild migrating fish provided a large sample size from a wide range of species that were extremely motivated to migrate. An experimental *in situ* approach provided information on fish behavioural responses to altered hydraulic slope, swimming ability of many wild migrating species and preliminary design criteria that could be immediately applied to similar sites, although further work to optimize fishway performance is required. These aspects of fish behaviour are difficult to replicate under controlled conditions when seeking to apply results in highly diverse systems.

ACKNOWLEDGEMENTS

This study was funded by the Australian Centre for International Agricultural Research and Industry and Investment NSW. Many people contributed to the success of this project. Local villagers from Pak Peung are thanked for contributing to field and data collection activities and are also thanked for providing access to the floodplain regulator. Mr Vone, Ms Nok and Ms Anna are expressly thanked for providing countless hours of assistance with fieldwork, data collection, fishway repairs and transport to and from the experimental site. Mr Jarrod McPherson, Ms Alana O'Brien, Mr Sileum, Mr Phousone and Mr Thanvone provided assistance with fieldwork and data entry activities. Dr Chris Barlow, Dr Bob Creese and two anonymous referees are thanked for useful comments on an earlier draft of the manuscript.

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