Universidad de Concepción

Facultad de Ciencias Ambientales
Programa de Doctorado en Ciencias Ambientales con mención en Sistemas Acuáticos Continentales

Development of fishways for longitudinal connectivity of Chilean rivers threatened by small-scale hydropower plants

Tesis para optar al grado de

Doctor en Ciencias Ambientales con mención en Sistemas Acuáticos Continentales

ANITA ALEJANDRA LABORDE GARCÍA

CONCEPCIÓN-CHILE
2022

Universidad de Concepción

Facultad de Ciencias Ambientales
Programa de Doctorado en Ciencias Ambientales con mención en Sistemas Acuáticos Continentales

Development of fishways for longitudinal connectivity of Chilean rivers threatened by small-scale hydropower plants

Tesis para optar al grado de

Doctor en Ciencias Ambientales con mención en Sistemas Acuáticos Continentales

ANITA ALEJANDRA LABORDE GARCÍA

Profesor Guía: Dr. Óscar Link Lazo

Departamento de Ingeniería Civil, Facultad de Ingeniería
Universidad de Concepción

CONCEPCIÓN-CHILE
2022

Para los inquietos y los que se interesan por comprender... porque cada día seamos más.

For the restless and those keen to understand... may there be more of us every day.

Comisión Evaluadora de Tesis de Grado:

Dr. Óscar Link
Director de Tesis
Departamento de Ingeniería Civil
Facultad de Ingeniería
Universidad de Concepción

Dra. Evelyn Habit
Cotutora de Tesis
Departamento de Sistemas Acuáticos Continentales
Facultad de Ciencias Ambientales
Universidad de Concepción

Dr. Paul Kemp
Evaluador Externo
International Centre for Ecohydraulic Research
Faculty of Engineering Physical Sciences
University of Southampton

Dr. Mauricio Aguayo
Evaluador Interno
Departamento de Sistemas Acuáticos
Facultad de Ciencias Ambientales
Universidad de Concepción

Dr. Claudio Valdovinos
Evaluador Interno
Departamento de Sistemas Acuáticos
Facultad de Ciencias Ambientales
Universidad de Concepción

AGRADECIMIENTOS - ACKNOWLEDGMENTS

A Óscar, Evelyn y Paul por interesarse por la ciencia y hacerla parte de sus vidas, por contagiarme y permitirme trabajar juntos. Por ser guías, motivadores y apoyo.

A Don René, Tote, Aliro y Waldo, por el apoyo, compañía y enseñanzas cuando hizo falta.

A los de siempre, por ser y estar.

To Óscar, Evelyn and Paul for their passion for science and for making it a part of their lives; for getting me involved and for allowing me to work with them. For their guidance, motivation and support.

To Don René, Tote, Aliro and Waldo for their support, company and teaching whenever needed.

To my constants, for being and for being there.

CONTENT INDEX

TABLES INDEX

FIGURES INDEX

SUMMARY

Freshwater ecosystems have become severely fragmented by artificial instream structures. Significant efforts have been made to reconnect freshwater systems to support fish movement through the design and installation of dedicated fish passage structures, or fishways. However, fishway design is based on a traditionally unique focus on salmonids or a small number of species often from northern regions. As such, designs may not be effective in other parts of the world, such as the Southern Hemisphere. Particular examples include Australia, New Zealand and South America, where native species consist mainly of small-bodied fish, a term that refers to adult fish with a body length of up to 15 cm.

The present research is motivated by the need to develop novel and innovative approaches to advancing fishway mitigation technologies for small-bodied fish and small juveniles exposed to instream structures. The situation of Chilean native fish species is used as the basis of a case study for the development of fishways for small-bodied fish worldwide. Three fundamental research questions are raised. (1) Which is the target group for the development of fishways in Chile? (2) What is the swimming performance of target group species? (3) Is there a fishway configuration suitable for passage of the target group, and can that suitability be quantified?

Trichomycterus, *Diplomystes* and *Percilia* (the TDP group) were the most prevalent genera within the assemblages present at planned hydropower project sites in South Central Chile (present at 40% of the sites; Laborde et al., 2020). The TDP group is composed of two small-bodied fish species (*T. areolatus* and *P. irwini*) and a species that coexists alongside them in its juvenile stage (*D. nahuelbutaensis*, juveniles up to 15 cm; Arratia et al., 1983). All three are benthofagous and resident species. Consequently, the TDP group was identified as a target group for the facilitation of fish passage.

Swimming capacities of TDP group species were estimated based on information obtained from the literature concerning applicability of proposed dimensionless variables and a proposed correlation of swimming capacities with fish species characteristics. Results showed that the dimensionless swimming capacities of small-bodied and large-bodied fish species are not comparable, even for the same taxonomic order, suggesting scale effects. Results also showed that the distance design curve proposed by Peake (1997) and applied to *Percilia* suggests fish passage velocity of up to 41 cm/s^{-1} along a 100-metre-long fishway.

Based on a review of the literature, fishway baffle designs were identified as the most suitable for the TDP group. Consequently, three different fishway configurations were proposed and evaluated over a 4-metre-long prototype fishway: lateral baffles (treatment 1); baffle array (treatment 2); and alternating lateral baffles (treatment 3). Passage of individual fish and interspecific fish

groups was assessed. Performance was quantified as passage efficiency, percentage of attempts, and percentage of impingements. In general, results showed that baffles increased passage efficiency and decreased the percentage of impingements. The lateral baffles configuration (treatment 1) showed the highest passage efficiency for *T. areolatus* (efficiency of 70%, 30% and 0% for treatments 1, 2 and 3, respectively) and *P. irwini* (efficiency of 43%, 0% and 20% for treatments 1, 2 and 3, respectively). In individual and interspecific group experiments, fish passage performance metrics in the lateral baffles configuration were not significantly different for *T. areolatus*, *P. irwini* and *D. nahuelbutaensis*. As such, lateral baffles constitute the optimum multi-species fishway design for small-bodied fish. Group passage efficiency in the lateral baffles configuration was 37%.

INTRODUCTION

Disruption of river connectivity due to instream structures has contributed to the population decline of many fish species around the world (Birnie-Gauvin et al., 2019). The need to maintain river connectivity and establish fish migration pathways through these structures has resulted in the development of fish passages, also known as fishways. This scientific solution relies on the theory of providing additional hydraulic structures to ensure that water velocities and depths are matched with the requirements of the target fish (Katopodis and Williams, 2012). Various fish passage solution types have been proposed and tested with fish found commonly in northern temperate regions, and particularly with highly prevalent or economically important species (Noonan et al., 2012; Kemp, 2016). However, research findings and remediation solutions for these species do not necessarily extrapolate to other species (Goodrich et al., 2018; Silva et al., 2018). This is particularly true for small-bodied fish, a term that refers to adult fish with a total body length of up to 15 cm. Small-bodied fish are present around the world; however, they are frequently endemic to regions of the southern temperate zone, particularly Australia (Watson et al., 2019), New Zealand (Magaju et al., 2020), southern South America (Link et al., 2017; Laborde et al., 2016; Link and Habit, 2015) and Southern Africa (Boubeé et al., 1999; Cussac et al., 2009). A significant lack of systematic, distributional and ecological information for these species has frequently been noted (e.g., Laborde et al., 2016; Franklin and Gee, 2019; Watson et al., 2019). This lack of knowledge of habitat requirements that could inform the design of fishways and the development of effective solutions for unimpeded small-bodied fish passage is compounded by pressure exerted by rapid economic expansion and land development (Wilkes et al., 2017; Habit et al., 2018).

Low-head structures (e.g., small hydropower plants – or SHPs – and culverts) have shown negative impacts on fish movement that are comparable to those of large structures, especially when the effects are considered cumulatively (Gibson et al., 2005). For example, Franklin and Gee (2018) showed a significant effect of small structures on river connectivity, with almost 12% of the New Zealand river network (based on an incomplete census of structures) being hindered by culverts. The present research focuses on Chile, a region that has been generating considerable attention in terms of hydropower exploitation, as it comprises 10 high-gradient watersheds with an estimated 12.5 GW potential, most of which will be supplied by SHPs. Central Chile is also part of the Chilean ichthyogeographic province (*sensu* Dyer, 2000), a biodiversity hotspot (Myers et al., 2000) accommodating a unique and highly endemic fish fauna. Thus, of major concern are the potential fragmentation of the entire region and the cumulative effects of multiple projects built within the natural range of native species that are predominantly resident (Díaz et al., 2019). The Chilean situation exemplifies a complex worldwide environmental conflict, namely, how to sustainably develop hydropower potential while conserving native species.

To date, none of the planned projects in Chile have incorporated any mitigation technology to support longitudinal river connectivity. In order to develop effective mitigation technologies in an ecoregion with high endemism, the most appropriate group of target species must be selected in order to prioritise conservation efforts. For species conservation, the use of surrogate species is the strategy most commonly applied (Thornton et al., 2016). Consequently, the first research question is: **Which is the target group for the development of fishways in Chile?**

One of the greatest challenges in fish passage technology is the development of structures and design concepts suitable for a broad range of species (Russon and Kemp, 2011; Watson et al., 2018; Romao et al., 2021). The design of effective fishway facilities must be informed by ecohydraulics, integrating factors both physical (hydrology, hydraulics and habitat morphodynamics) and biological (life cycle requirements, migration behaviour and fish swimming performance, including capability, metabolism and kinematics) (Noonan et al., 2012; Katopodis and Gervais, 2016; Wang and Chanson, 2018). The hydraulic design of fishways requires basic information on fish swimming capabilities. Swimming performance is especially important in determining when velocities are likely to exceed endurance (e.g., for weirs) or burst (e.g., for gaps between pools) swimming velocities (Russon and Kemp, 2011). Without reference to other biological criteria, the use of critical swimming velocity for fishway design rests on assumptions regarding swimming performance (Laborde et al., 2016). Katopodis (1994) proposed velocity- and time-dimensionless variables to generalise data. Katopodis and Gervais (2016) created a swimming performance database of 131 fish species using data extracted from the literature (mainly large-bodied fish species). Watson et al. (2019) showed that fish body length and depth station correlated with their swimming performance. Thus, lessons learned over time and knowledge accrued from comprehensive studies have improved understanding, providing instructive paradigms for small-bodied fish habitat reconnection (Jager et al., 2016; Katopodis and Williams, 2016). This raises the second research question: **What is the swimming performance of target group species?**

Evaluation of new designs specifically geared towards small-bodied fish is also required (Knapp et al., 2019). Locally confined low-velocity zones are thought to play a significant part in the successful upstream passage of small-bodied fish (Wang et al., 2016; Zhang and Chanson, 2018). Due to their size, small-bodied fish can more readily make use of these smaller flow features. Low-velocity zones should be evenly distributed, continuous, providing fish with rest areas along their path upstream. The discharge capacity of a given cross-section is less affected by the inclusion of locally confined low-velocity zones than by an overall reduction in water velocity for a complete cross-section (Zhang and Chanson, 2018). It does, however, lead to increased hydraulic roughness within the wetted surface of a structure (Ead et al., 2002; Baki et al., 2015). Engineering designs of various shapes, forms and arrangements have been developed and used to create fishways of different shapes, sizes and lengths (Muraoka et al., 2017; Rodgers et al., 2017; Goodrich et al., 2018; Wang and Chanson, 2018; Amaral et al., 2019; Johnson et al., 2019). A few unique solutions, such as using mussel-spat ropes as a form of baffling, have also been developed and tested for different species (David et al., 2014). Aside from conventional designs, various customised roughness elements, such as sloping baffles (Newbold et al., 2014), ventilated corner baffles (Cabonce et al., 2018; Sailema et al., 2019), longitudinal square beams (Watson et al., 2018) and other industrial designs (Baker and Boubeé, 2006) have also been developed and tested. Roughness elements of the same size and shape have been found to perform differently with changes in arrangement (Enders et al., 2017). Furthermore, performance for a given species has been found to vary between roughness elements of different types (Amtstaetter et al., 2017). Passage efficiency, being one of the most crucial aspects of fish passage solutions, is currently the most widely discussed topic in fish passage research (Noonan et al., 2012; Silva et al., 2018). Another factor to consider is that fish may abandon an ascent for behavioural reasons rather than due to limits to their swimming ability (Vowles et al., 2019). This background leads to the third research question: **Is there a fishway configuration suitable for passage of the target group, and can that suitability be quantified?**

HYPOTHESIS AND OBJECTIVES

Alterations in longitudinal river connectivity have a significant effect on fish populations. Reductions in the longitudinal habitat connectivity of native Chilean fish due to extensive hydropower development can be mitigated by the development of fish passage solutions, or fishways. Multi-species fishway design, which provides a solution to habitat fragmentation for several species simultaneously, is based on swimming capacities and behaviour. At the fishway scale it is expected that at least one individual would be able to successfully complete an upstream displacement.

The general objective of the present research is to establish a multi-species fishway solution to allow native Chilean fish species to overcome the barriers imposed by small hydropower plants (< 5 m in height). The general hypothesis is as follows: There is at least one fishway configuration that provides a solution to longitudinal river fragmentation for the assemblage potentially most affected by hydropower development in Chile.

In order to fulfil the overall objective and to test the general hypothesis, three research questions were posed, each accompanied by specific objectives and hypothesis tests.

1. **Which is the target group for the development of fishways in Chile?**

In order to respond to the question, we proposed the specific objective of identifying assemblages of native Chilean fish vulnerable to extensive hydropower development and the selection of a target assemblage (modal). We then specified the following hypothesis test: The most vulnerable assemblage will consist of those species with the greatest spatial distribution.

2. **What is the swimming performance of target group species?**

In order to respond to the question, we proposed the specific objective of estimating the fish swimming capacities of species belonging to the target assemblage. We then specified the following hypothesis test: Given that they belong to the same assemblage and coexist within the same habitats, the species that constitute the most vulnerable assemblage will have similar swimming capacities.

3. **Is there a fishway configuration suitable for passage of the target group, and can that suitability be quantified?**

In order to respond to the question, we proposed the specific objective of evaluating the effectiveness of three multi-species fishway configurations for the target assemblage. We then specified the following hypothesis test: Given that the target group consists of small-bodied species, passage performance will be lower than reported in the available literature and, as such, new metrics will be required in order to evaluate fishway suitability.

THESIS STRUCTURE

This thesis is motivated by the need for novel and innovative approaches to fishway mitigation technologies targeting small-bodied fish and species which, at the juvenile stage, have a body length of up to 15 cm.

The thesis makes a case study of Chile, a region that has been generating considerable attention in terms of hydropower exploitation. The country comprises 10 high-gradient watersheds with an estimated 12.5 GW potential, most of which would be supplied by SHPs. Central Chile is also part of the Chilean ichthyogeographic province (*sensu* Dyer, 2000), a biodiversity hotspot (Myers et al., 2000) accommodating a unique and highly endemic fish fauna. Thus, of major concern are the potential fragmentation of the entire region and the cumulative effects of multiple projects built within the natural range of native species that are predominantly resident (Díaz et al., 2019). To date, none of the planned project in Chile have incorporated any mitigation technology to support longitudinal river connectivity. The Chilean situation exemplifies a complex environmental conflict that is common worldwide, namely, how to sustainably develop hydropower potential while conserving native species.

The research is presented in three chapters, each of which seeks to answer one of the three research questions in association with the objectives of the thesis, as shown in Figure 0-1.

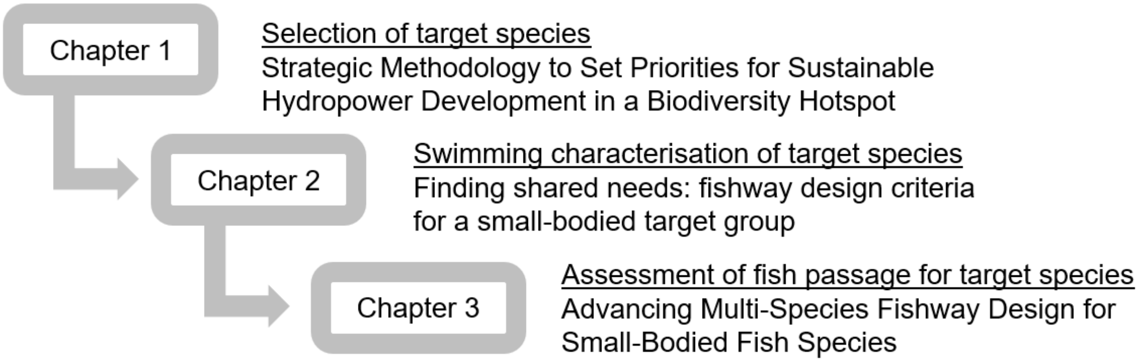


Figure 0-1 Schematic representation of the thesis

In order to answer the first research question – “Which is the target group for the development of fishways in Chile? – the first chapter presents a methodology for the setting of conservation priorities for sustainable hydropower development in Chile by analysing the characteristics of Chilean native species and of planned hydropower projects. Hydroelectric projects were characterised and the habitat distribution of species was estimated. Assemblies of species that would be affected by each of the projects were identified. According to this information, the hydroelectric projects were classified into three groups: (1) projects that do not require mitigation because they would allow the passage of species, or because there would be no affected fish species; (2) projects that require mitigation that is not considered to be technically feasible due to their large scale; and (3) projects that require mitigation that is considered to be technically feasible. For the latter, a functional criterion based on habitat use was selected to identify the target group, as assemblages were defined according to the most frequently occurring species at each planned project site.

The second chapter seeks to answer the second research question – “What is the swimming performance of target group species?” – and presents a review of the literature on swimming performance of small-bodied fish species. Swimming performance information was reviewed specifically for the genera *Percilia*, *Trichomycterus* and *Diplomystes*, encompassing large-bodied and small-bodied fish species. Swimming capacities were estimated based on information obtained from the literature concerning applicability of proposed dimensionless variables and a proposed correlation of swimming capacities with fish species characteristics. The applicability of the generalised curves presented by Katopodis and Gervais (2016) for small-bodied species was analysed. Then, those species with similar characteristics to the species present in the TDP group were reviewed. Swimming capacities for *T. areolatus*, *P. irwini* and *D. nahuelbutaensis* were estimated based on previous results and according to the hypotheses posed by Katopodis and Gervais (2016) and Watson et al. (2019). Finally, based on estimated swimming performance and body length range, the expected distance design curve as proposed by Peake (1997) was calculated.

In the third chapter, which seeks to answer the third research question – “Is there a fishway configuration suitable for passage of target group species?” – three different fishway configurations were proposed and evaluated over a 4-metre-long prototype fishway: lateral baffles (treatment 1), baffle array (treatment

2), and alternating lateral baffles (treatment 3). Passage of individual fish and interspecific fish groups was assessed. Performance was quantified as passage efficiency (i.e., the number of successful attempts by fish to pass), percentage of attempts, and percentage of impingements. First, a comparison was made between the passage performance of individuals moving upstream as they attempted to pass a carpet and unmodified (control) prototype fishway with three different baffle configurations: lateral baffles, baffle array and alternating lateral baffles. This allowed identification of the baffle configuration with the highest passage efficiency. We then tested upstream movement performance for each species group (TDP group), passage performance in the control configuration, and passage performance in the baffle configuration with highest passage efficiency. Passage performance in experiments involving individuals and species groups were compared. If the performance of the species was not modified by the presence of other-species individuals, the fishway was considered to be suitable for multiple species.

CHAPTER 1: STRATEGIC METHODOLOGY TO SET PRIORITIES FOR SUSTAINABLE HYDROPOWER DEVELOPMENT IN A BIODIVERSITY HOTSPOT

This chapter is based on:
Laborde, A., Habit, E., Link, O., Kemp, P. (2020)
Strategic methodology to set priorities for sustainable hydropower development in a biodiversity hotspot.
Science of the Total Environment, 714, 136735.

Strategic Methodology to Set Priorities for Sustainable Hydropower Development in a Biodiversity Hotspot

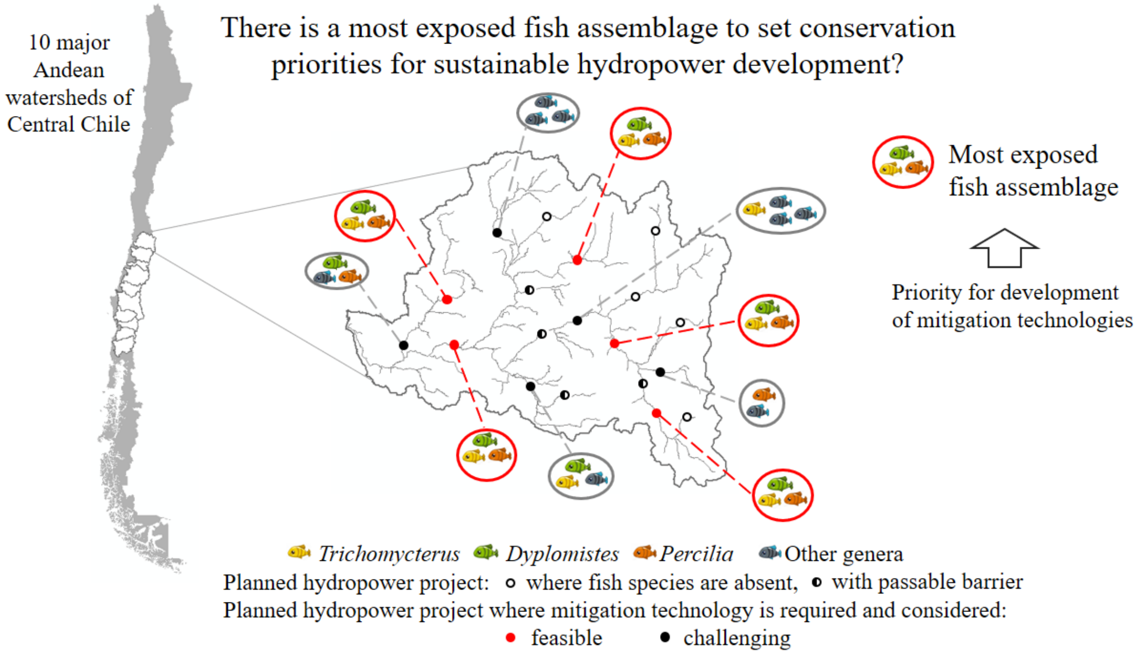
A. Laborde[a], E. Habit[a], O. Link[b], P. Kemp[c]

[a] *Department of Aquatic Systems, Faculty of Environmental Sciences and EULA Centre, Universidad de Concepción, Concepción, Chile*

[b] *Civil Engineering Department, Universidad de Concepción, Concepción, Chile*

[c] *International Centre for Ecohydraulic Research, Faculty of Engineering Physical Sciences, University of Southampton, UK*

Graphical abstract



Abstract

Massive exploitation of freshwater systems for hydropower generation in developing countries is challenging sustainability due to cumulative environmental impacts in regions with high endemism. Habitat fragmentation is recognised as a major impact on river ecosystems. The nature and magnitude of connectivity loss depend on characteristics of the hydropower projects, and of the threatened fish communities. In areas where appropriate mitigation technology is lacking, there is a need to identify the fish species that are most at risk to better concentrate efforts. This paper aimed to set conservation priorities for sustainable hydropower development by analysing native fish species and project characteristics. The Chilean ichthyogeographic province, an ecoregion with high endemism and home to largescale hydropower development, is taken as a case study. Using overlapping information on the characteristics of 1124 hydropower projects and distribution of native fish species, we identified three project categories based on their need for mitigation. These were projects where mitigation was considered a) not required (15%), b) required and feasible (35%), and c) required but challenging (50%). Projects where mitigation was not required were located at sites where native fish were absent and/or where water intakes allowed fish to pass. Interestingly, projects where mitigation was considered feasible were inhabited by a species assemblage that comprised the genera *Trichomycterus*, *Diplomystes* and *Percilia*, and the species *Ch. pisciculus* and *B. maldonadoi*. This finding emphasises the need to develop a multi-species fishway design that can accommodate this group. Projects where mitigation would be difficult to achieve were located at sites with a variety of different assemblages present, thus making the implementation a standard fishway solution challenging and site-specific. The study advances understanding of the need to develop mitigation strategies and technologies in ecoregions of high endemism threatened by hydropower, and to prioritise the construction of planned projects.

Keywords: Dams, native fish, conservation, mitigation, fish passage, Chile.

Introduction

Worldwide, urgent reduction of greenhouse gases due to climate change motivates the development of non-conventional renewable energies to satisfy increasing energy demand. Globally, hydropower is the leading renewable energy source accounting for 18% of total electricity supply (Kumar et al., 2011), and its development has experienced a recent boom with small and medium-sized dams (1–100 MW) dominating in number (> 75%) (Zarfl et al., 2015). The global installed capacity of small hydropower projects (SHP, i.e., installed capacity less than 20 MW) is estimated to be 75 GW, with an additional 173 GW of potential remaining to be developed (SHW, 2013). At the same time, hydropower can severely impact freshwater ecosystems (Zhou et al., 2015 Lees et al., 2016, Winemiller et al., 2016, Latrubesse et al., 2017).

River fragmentation arguably has had the most profound ecological effects and has been considered the greatest threat to riverine biodiversity (Vörösmarty et al., 2010), and primary cause for the decline of freshwater ichthyofauna (Romao, 2017). Barriers to migration can restrict access to critical habitats required for foraging and feeding, predator avoidance, shelter, and spawning (Gibson et al., 2005), and ultimately lead to a reduction in recruitment, population decline, and a loss of biodiversity (Franklin and Bartels, 2012). There are many examples of decline, and occasional extinction of the fish population when rivers are dammed (e.g., Jelks et al., 2008; Vörösmarty et al., 2010; Radinger and

Wolter, 2014). Negative effects, such as disruption of gene flow (e.g., Frankham, 2015; Valenzuela et al., 2019); physical habitat disturbance (e.g., Howell, 2006); and local extinction due to stochastic demographic processes (e.g., Stephens and Sutherland, 1999), have not been confined only to migratory fish, but also resident species (Wilkes et al., 2018). The majority of Chilean native fish species are resident and do not undertake extensive migration between clearly separated critical habitats, yet the movement of individuals and the genetic information they carry is critically important for population viability (Wilkes et al., 2018). This was recently acknowledging for *Percilia irwini*, endemic Chilean species (Valenzuela et al., 2019). Fish have been threatened on all continents, with nearly 50% of freshwater ecoregions (397 assessed) obstructed by large- and medium-sized dams (Liermann et al., 2012).

The nature and magnitude of connectivity loss depends on the characteristics of the hydropower projects and the impacted ecosystem. Although the precise design of hydropower projects depends on site conditions, SHP typically diverts flow in the order of a few cubic meters per second (< 100 m^3/s), and bottom intakes such as *tyrolean* weirs, or lateral intakes are typically used. The small dams associated with these intakes, commonly varying between 2 and 20 m height, can severely fragment habitat (Link and Habit, 2015). Furthermore, the magnitude of impacts on the aquatic biota depends on diversity, sensitivity, resistance and resilience status (Ziv et al., 2012; McCluney et al., 2014). Sites inhabited by fish communities composed of endemic and/or vulnerable species are at greatest risk, and if developed impacts must be mitigated.

In an attempt to counteract the negative effects of habitat fragmentation, a wide variety of devices have been installed at river barriers to restore connectivity, with fishways being the most common, enabling fish to bypass the impediment under their own effort (Clay, 1995). Current fish pass design is based on a traditional focus on only one or a few species, often salmonids in northern temperate regions, and thus they may not be effective in other regions, such as in the Southern Hemisphere (Link and Habit, 2015; Kemp, 2016; Franklin and Baker, 2016). The application of traditional fishway solutions to other geographical regions has been challenging for many reasons, largely related to differences in species richness and abundance, diversity of life histories, body morphologies, swimming capabilities and behaviours when compared to the target species for which they were designed (Kemp, 2016). Over the last decade, this bias has been recognised and now efforts have been made to develop fishways for a wider range of target species (Santos et al., 2014; Branco et al., 2017; Romao et al., 2018).

To develop an effective mitigation technology in ecoregions with high endemism there is a need to select the most appropriated group of target species in order to prioritise conservation efforts. Conservation managers often use one or a small number of species as surrogates to help them tackle conservation problems (Caro et al., 1999; Thornton et al., 2016). Species surrogate is a blanket term that encompasses several concepts including indicator species, umbrella species, key-stone species and flagship species (Fleishman et al., 2000; Caro, 2010; Thornthon et al., 2016). Surrogate species are employed to indicate the extent of various types of anthropogenic influence (Stolte and Mangis,1992) or to track populational changes in other species. Surrogate species are also used proactively to locate areas of high biodiversity (Ricketts et al., 1999) or to act as “umbrellas” for the requirements of sympatric species (Berger, 1997). Finally, surrogate species may be used as flagships in a socio-political context for attracting public attention and funding to tackle a larger environmental issue (Dietz et al., 1994). In contrast, a keystone species is an ecological concept that is used to describe a species whose impact on the community or ecosystem is disproportionately large relative to its abundance (Power et al., 1996). Meffe and Berra (1988) introduced the concept of a selecting core group of species related to their presence, abundance, i.e., persistence and stability of the assemblage. In the case of developing mitigation technologies to restore longitudinal habitat connectivity, such as fishways, the core group concept by Meffe and Berra (1988) seems to be the best available approach to identify the species most exposed to the impacts of hydropower plants, allowing a massive technological solution.

This study aimed to develop a methodology to set conservation priorities for sustainable hydropower development in Chile by analysing the characteristics of Chilean native species and planned hydropower projects. This region has been generating considerable attention in terms of hydropower exploitation, as it comprises 10 high gradient watersheds with an estimated 12.5 GW potential

(Ministry of Energy, 2015), most of which would be supplied by SHPs. Central Chile is also part of the Chilean ichthyogeographic province (*sensu* Dyer 2000), a biodiversity hotspot (Myers et al., 2000) accommodating a unique and highly endemic fish fauna. Thus, a major concern is the potential fragmentation of the entire region and the cumulative effects of multiple projects built within the natural range of native species that are predominantly resident (Díaz et al., 2019). To date, none of the planned projects has been designed to incorporate any mitigation technology. The Chilean situation exemplifies a complex environmental conflict that is common worldwide, namely, how to sustainably develop hydropower potential while conserving native species. Considering central Chile as a case study, the first objective was to develop a database for the distribution of native fish species in these watersheds. The second objective was to identify hydropower projects where fish populations would likely be impacted and superimpose this on the information-maintained fish database. This would enable identification of projects according to the need for mitigation for habitat fragmentation, based on the magnitude of the impact and feasibility of applying appropriate technology. Hydropower projects were classified into sites where mitigation is (1) not required, (2) required and considered feasible, and (3) required but considered challenging. The characteristics of the project groups and presence of fish were analysed.

Methodology

Strategic methodology to set priorities for sustainable hydropower development

The planned hydropower projects were grouped into projects: a) where fish are absent due to their location, as native fish are absent at altitudes above 1500 m.s.l. (Vila et al., 1999); b) with passable barriers when the water intake does not block or partially block the channel cross-section, i.e., lateral water intakes without dam; c) with fish data, and d) without fish data.

For the project groups with fish data and impassable barriers, present species at each site were identified as a "fish assemblage", including cases where only a single species was recorded. Thus, a functional selection criterion was applied based on habitat use (Meffe and Berra, 1988). Species composition and most frequent genera of fish assemblages at each project were identified. As the swimming capabilities of Chilean native species is not well known (Laborde et al., 2016), the potential fishway passage performance was estimated based on position typically held in the water column (i.e., benthic or pelagic; Kapitzke et al., 2010), body size (i.e., less or more than 15 cm when adults; Katopodis and Gervais, 2012), and swimming mode (i.e., angulliform, subcarangiform, carangiform; Sfakiotakis et al., 1999; Breder, 1926; Lacey et al., 2012; Link and Habit, 2015). Assemblages composed of the most frequent genera and species with similar fish passage performance were considered to be the target group in order to set bounded requirements for future development of mitigation technologies. Similarity in body size is related to similar swimming capabilities (e.g., Sanz-Ronda et al., 2015). Similarity in position in the water column will inform the positioning of obstacles for energy dissipation. Similarity in swimming mode is related to fish behaviour, specifically, to how fish tackle obstacles (surpassing, over the top; dodging, to the side; etc.). The presence of a target group promotes the implementation of a mitigation technology since it involves a generalised solution: a unique design with extensive application. Only Chilean native fish species impacted by hydropower projects are included.

Generalisation of results obtained for the project groups with impassable barriers and fish data, to those projects with impassable barriers without fish data, was analysed based on statistical differences between both groups considering geographical unit, watershed and Strahler's order, capacity, dam height, turbine, and intake type, applying ANOSIM test on a Euclidean distance resemblance matrix on normalised variables. The results obtained are used to estimate the magnitude of the environmental conflict in the study area, assuming assemblages present in project groups with impassable barriers and that fish data will occur in a similar manner at projects with impassable barriers without fish data.

Statistical differences between projects where mitigation is not required, required and considered feasible, and required but considered challenging were determined to define which hydropower characteristics (i.e., geographical unit, watershed, Strahler's order, capacity, dam height, turbine, and intake type) contribute most to the differences among these three categories, applying a SIMPER routine (Warwick and Clarke, 1998). SIMPER performs pairwise comparisons of groups of sampling units and finds the average contributions of each projects to the average overall Bray-Curtis dissimilarity. All statistical analyses were performed using Primer-E (v.7.15; Clarke and Gorley, 2015). Results were considered significant if $p \leq 0.005$, and marginally significant if $0.05 < p \leq 0.07$.

Study area

The study focused on the 10 major Andean watersheds of Central Chile (between 32° and 41° Lat. S), from the Maipo River in the North to the Bueno River in the South. Approximately 90% of the area is drained by rivers flowing predominantly from East to West with a total length of approximately 200 - 400 km, Strahler's orders up to eight, and annual mean discharges at the mouth of between 100 and 1000 m^3/s. All fluvial systems follow the same pattern, flowing from the Andes to the Coast (with river longitudinal slopes in the Andes between 5-10%) through the Central Valley (Link and Habit, 2015).

The exploitable hydropower in the study area was estimated to be 12,338 GW distributed across 1124 sites (Ministry of Energy, 2015). Location (intake and outlet), capacity, head, and discharge of planned hydropower projects were obtained from the Ministry of Energy (2015) (Figure 1). Geographical units (Andean mountain range, Central valley, and Costal chain of hills), drainage networks and their properties, such as river length, Strahler's order, and elevation, were computed using GIS software (ArcGIS 10.3) from SRTM satellite images. Characteristics of the stretch of the river where planned projects are located, such as the number of channels, channel width, and longitudinal profile type (e.g., straight or curve) were estimated using Google Earth Pro.

Historical data provided by the Ministry of Environment (2015) of the presence/absence of native fish species collected at sampling sites (included over 3,500 records) in the study area was used to calculate distribution and species richness for each river network (Figure 1- 1).

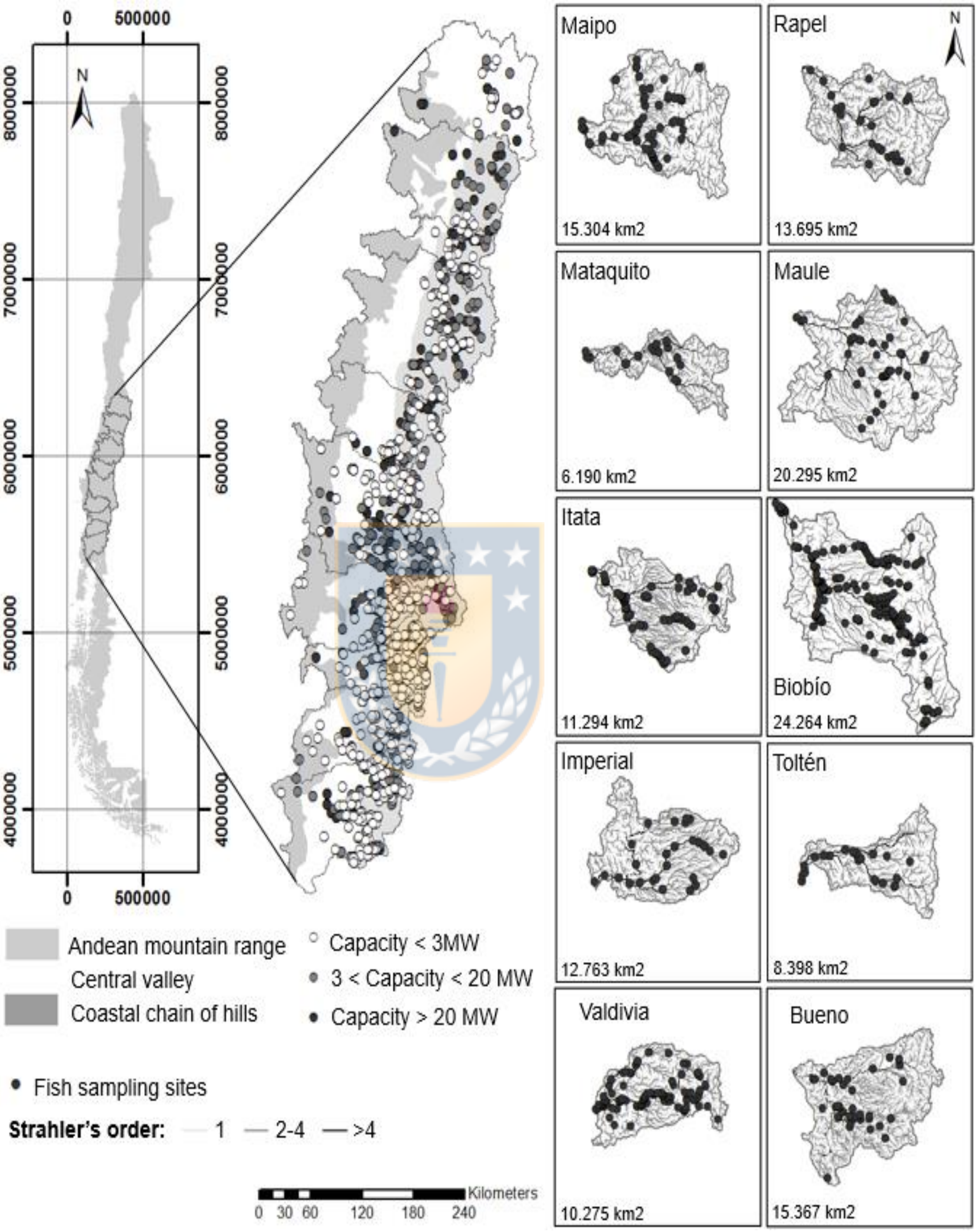


Figure 1-0-1. Location of the study area in Chile (a), planned hydropower projects along the 10 river watersheds (b), and fish sampling sites within each of the river watersheds from North to South (c).

Species distribution, species richness and conservation status

Fish distribution was determined by interpolation of the species presence between sampling sites, considering habitat use and life history (Habit et al., 2005, 2006; García et al., 2012). Conservation status was obtained from MMA (2018). Endemism to the Chilean territory and the study area was obtained from Habit et al. (2006) and Vila and Habit (2015).

Hydropower projects

Hydropower projects were classified according to their geographical unit (distinguishing sites in the Andes, Central Valley and Coastal chain of hills), Strahler's order, capacity (installed capacity, C, in MW), dam height (m), turbine and intake type. Dam height was estimated based on project capacity and the distance between the intake and outlet, L (m). Two classes of dam height, h, were distinguished according to their relevance for habitat fragmentation:

$h < 20$ m if:

$C < 20$ MW

$C < 50$ MW and $L > 500$ m

and $h > 20$ m if:

$C > 50$ MW and $L \leq 200$ m

C ≥ 150 MW and 500 m ≤ L ≤ 15000 m

The turbine type (Pelton, Francis, and Kaplan) was determined from a standard turbine selection chart according to available discharge and head. Intake type (Lateral intake with barrier, i.e., dams with weir or gate; Tyrolean intake, i.e., bottom intake; and Lateral intake without a barrier) was estimated based on characteristics of the stretch of the river: number of channels on the reach, N, channel width, W (m), longitudinal profile type, P, e.g., straight or curve.

Lateral intake with barrier if:
N > 1
N = 1 and W > 15 m and P = straight
N = 1 and W ≤ 5 m and P = curve
Tyrolean intake if:
N = 1 and W ≤ 15 m and P = straight
and Lateral intake without a barrier if:
N = 1 and W > 5 m and P = curve

Results

Species distribution, species richness and conservation status

The study area hosts 31 (65.9%) of the 47 Chilean freshwater fish species (Table 1- 1), all are resident. These species belong to 7 families and comprise 16 genera, of which 14 are Teleosts and 2 are Agnatha (lamprey). Of all the species present in the study area, 35.4% are smaller than 15 cm total length (TL) when adult and only 19.4% reach adult sizes > 25 cm TL. The most abundant groups are the Siluriforms (9 species) and Osmeriforms (7 species). Other groups represented in the study area are Characiforms (4 species), Atheriniforms (4 species), Perciforms (4 species), Petromyzontiforms (2 species) and Mugiliforms (1 species). 74.2% of the fish species are endemic to the study area, 38.7% and 48.3% are classified as Endangered and Vulnerable, respectively (Table 1- 1). Biobío and Valdivia river basins showed the highest species richness (17 species each). The Biobío basin also contains two endemic species, namely: *Trichomycterus chiltoni* and *Percilia irwini*. Species more widespread within the study area were *Trichomycterus areolatus*, *Basilichthys microlepidotus*, *Percilia gillissi*, *Percichthys trucha*, and *Galaxias maculatus* (with more than 2000 km. of distribution length each).

Table 1-0-1. Characteristics of the native fish species present in the study area. Species distribution length represent the total length of presence within all river basins inhabited. River basin names in bold correspond to basins where the species were exposed to at least one hydropower project.

				Endemic to		
Order	**Species**	**Species distribution length (km)**	**Conservation status**	**Chilean territory**	**Study area**	**River basin with presence of the species**
Characiformes	*Cheirodon kiliani*	38.1	Endangered	Yes	Yes	Valdivia
Siluriformes	*Diplomystes chilensis*	11.5	Endangered	Yes	Yes	Maipo
Osmeriformes	*Brachygalaxias gothei*	7.96	Vulnerable	Yes	Yes	Maule
Mugiliformes	*Mugil cephalus*	95.1	Less concern	No		Maipo, Mataquito, Itata, Biobío
Osmeriformes	*Aplochiton marinus*	26.4	Endangered	No		Valdivia
Atheriniformes	*Odontesthes brevianalis*	23.4	Vulnerable	Yes	No	Maipo
Atheriniformes	*Odontesthes itatanum*	9.93	Vulnerable	Yes	Yes	Itata
Characiformes	*Cheirodon pisciculus*	685.7	Vulnerable	Yes	No	**Maipo, Rapel, Mataquito**
Siluriformes	*Hatcheria macraei*	75.8	Vulnerable	No		Imperial, **Valdivia, Bueno**
Siluriformes	*Diplomystes camposensis*	273.4	Endangered	Yes	Yes	**Valdivia,** Toltén
Osmeriformes	*Brachygalaxias bullocki*	392.3	Vulnerable	Yes	No	**Itata,** Biobío, **Imperial, Valdivia,** Toltén, **Bueno**
Petromy-zontiformes	*Mordacia lapicida*	641.6	Endangered	Yes	No	Itata, **Biobío, Toltén, Valdivia**
Siluriformes	*Trichomycterus chiltoni*	172.5	Endangered	Yes	Yes	**Biobío**
Characiformes	*Cheirodon australe*	514	Vulnerable	Yes	Yes	**Bueno, Toltén, Valdivia**
Siluriformes	*Nematogenys inermis*	256.3	Vulnerable	Yes	Yes	Maipo, **Rapel, Maule,** Itata,

						Biobío, Imperial
Osmeriformes	*Aplochiton zebra*	247.1	Endangered	Yes	No	**Bíobío, Valdivia,** Toltén, **Bueno**
Perciformes	*Percichthys melanops*	372.6	Vulnerable	Yes	Yes	**Maipo,** Mataquito, Maule, Itata, **Biobío, Toltén**
Osmeriformes	*Aplochiton taeniatus*	227.7	Endangered	No		**Toltén, Valdivia,** Bueno
Osmeriformes	*Galaxias platei*	381.4	Less concern	No		**Valdivia,** Toltén, **Bueno**
Characiformes	*Cheirodon galusdae*	1494.2	Vulnerable	Yes	Yes	Mataquito, **Maule, Itata, Biobío, Imperial**
Atheriniformes	*Odontesthes mauleanum*	914.6	Vulnerable	Yes	No	Rapel, Mataquito, Maule, Itata, **Biobío,** Imperial, **Toltén, Valdivia, Bueno**
Siluriform	*Bullockia madonadoi*	907.7	Endangered	Yes	Yes	**Itata, Biobío, Imperial, Toltén**
Petromyzontiformes	*Geotria australis*	1651.2	Vulnerable	No		Itata, **Biobío, Imperial, Toltén, Valdivia, Bueno**
Siluriformes	*Diplomystes incognitus*	1084.5	Non classified		Yes	**Rapel, Mataquito, Maule, Itata**
Siluriformes	*Diplomystes nahuelbutaensis*	957.7	Endangered	Yes	Yes	**Biobío, Imperial**
Perciformes	*Percilia irwini*	1219.1	Endangered	Yes	Yes	**Biobío**
Osmeriformes	*Galaxias maculatus*	2250.2	Maule to north: Vulnerable; Biobío south: Less concern	No		Maipo, **Itata, Biobío, Imperial, Toltén, Valdivia, Bueno**
Perciformes	*Percilia gillissi*	3164.6	Endangered	Yes	No	**Maipo, Rapel, Mataquito, Maule, Itata,**

						Imperial, Toltén, Valdivia, Bueno
Perciformes	*Percichthys trucha*	2909.3	Near threaten	No		Maipo, **Rapel, Mataquito, Maule, Itata, Biobío, Imperial,** Toltén, **Valdivia, Bueno**
Atheriniformes	*Basilichthys microlepidotus*	3520	Vulnerable	Yes	No	**Maipo, Rapel, Mataquito, Maule, Itata, Biobío, Imperial, Toltén, Valdivia, Bueno**
Siluriformes	*Trichomycterus areolatus*	4701.4	Vulnerable	No		**Maipo, Rapel, Mataquito, Maule, Itata, Biobío, Imperial, Toltén, Valdivia, Bueno**

Hydropower projects and the need for mitigation technology

The exploitable hydropower in the study area was 12,338 GW distributed across 1124 sites. From those sites, 165 (15%) projects were located above 1500 m.s.l. and/or have optimum passability (i.e., lateral intake without barrier). Therefore, for 959 (85%) of projects, fish species would be impacted. From these sites, 219 have fish data and 740 do not.

Projects sites where mitigation is not required

A total of 165 planned projects do not requires mitigation. Of these sites, 43 were located above 1500 m.s.l., and 122 showed an intake with optimum passability. Their exploitable hydropower was 1,532 GW.

Projects where mitigation is not required were mainly located on the Andes mountain range (81%), concentrated in the Maule and Biobío river basin (45%), and in reaches with 2-4 Strahler’s order (76%). The predominant characteristics of these projects were a capacity of 3-20 MW (48%), dam height of less than 20 m (87%), Francis turbine (72%) and lateral intake without a barrier (77%) (Figure 1- 3).

Project sites where mitigation is required and considered feasible

The 31 species present in the study area formed a total of 83 assemblages which comprised up to 13 species. The most frequent genera in the different assemblages were: *Trichomycterus*, *Diplomystes*, and *Percilia*, referred to as the TDP group. A total of 87 projects were planned at sites where only species belonging to the TDP group were present. All species belonging to this group were characterised as predominantly benthic, less than 25 cm total length when adult, and exhibing subcarangiform and carangiform swimming modes (Link and Habit, 2015). Compared to the TDP group, *Cheirodon pisciculus* and *Bullockia maldonadoi* were considered to have similar fishway passage performance.

Consequently, the TDP group, *Ch. pisciculus* and *B. maldonadoi* were defined as the core group of species on which development of a technical solution that could best mitigate fragmentation at the highest number of planned projects should be based. From the 219 project sites that affect fish and for which fish data is available, 90 projects (41%) maintain the core group, with an exploitable hydropower potential of 1,824 GW.

Project sites where mitigation is required and considered feasible were mainly located in the Andes mountain range (85%) of the Maule, Itata and Biobío river basin (71%), and reaches of 2-4 Strahler's order (83%). The predominant characteristics of these projects were capacity of 3-20 MW (49%), dam height of less than 20 m (74%), Francis turbines (87%), and lateral intake with a barrier (88%) (Figure 1- 3).

Project sites where mitigation is required and considered challenging

A total of 129 projects are planned in river reaches represented by species other than the core group, with a variety of different assemblages that makes the development of a standard solution difficult (Supl. Material S1). This is because case-specific solutions would be required, particularly at sites with high local species richness (Figure 1- 2a). Furthermore, there was a positive and marginaly significant correlation between the number of planned hydropower projects and fish species richness in a river basin ($y = 12.68x - 53.69$, $R^2 = 0.356$, $p = 0.071$;

Figure 1- 2b). The Biobío river basin stands out with a high number of proposed projects overlapping with high species richness.

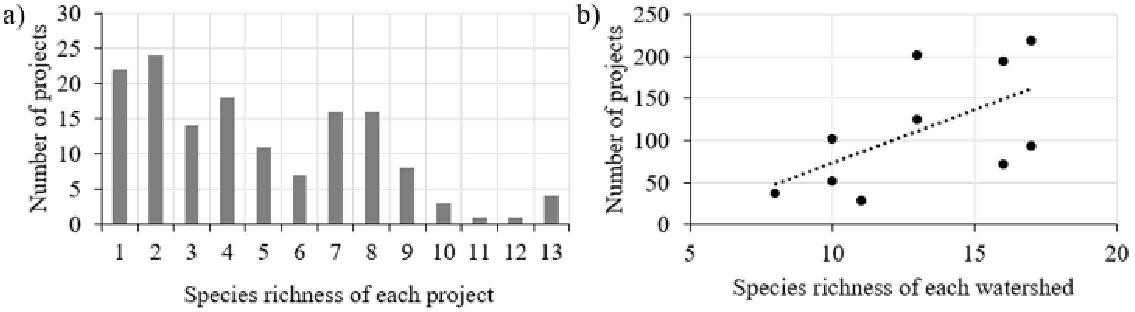


Figure 1-0-2. Relationship between number of projects and species richness of each project (a), mean species richness of each river basin (b).

Projects sites where mitigation is required and considered challenging were mainly located in the Andes mountain range (66%), concentrated in the Biobío and Valdivia river basin (58%), in reaches with 2-4 Strahler's order (64%). The predominant characteristics of these projects were capacity of less than 30 MW (39%), dam height of less than 20 m (75%), Francis turbine (76%) and lateral intake with a barrier (85%) (Figure 1- 1).

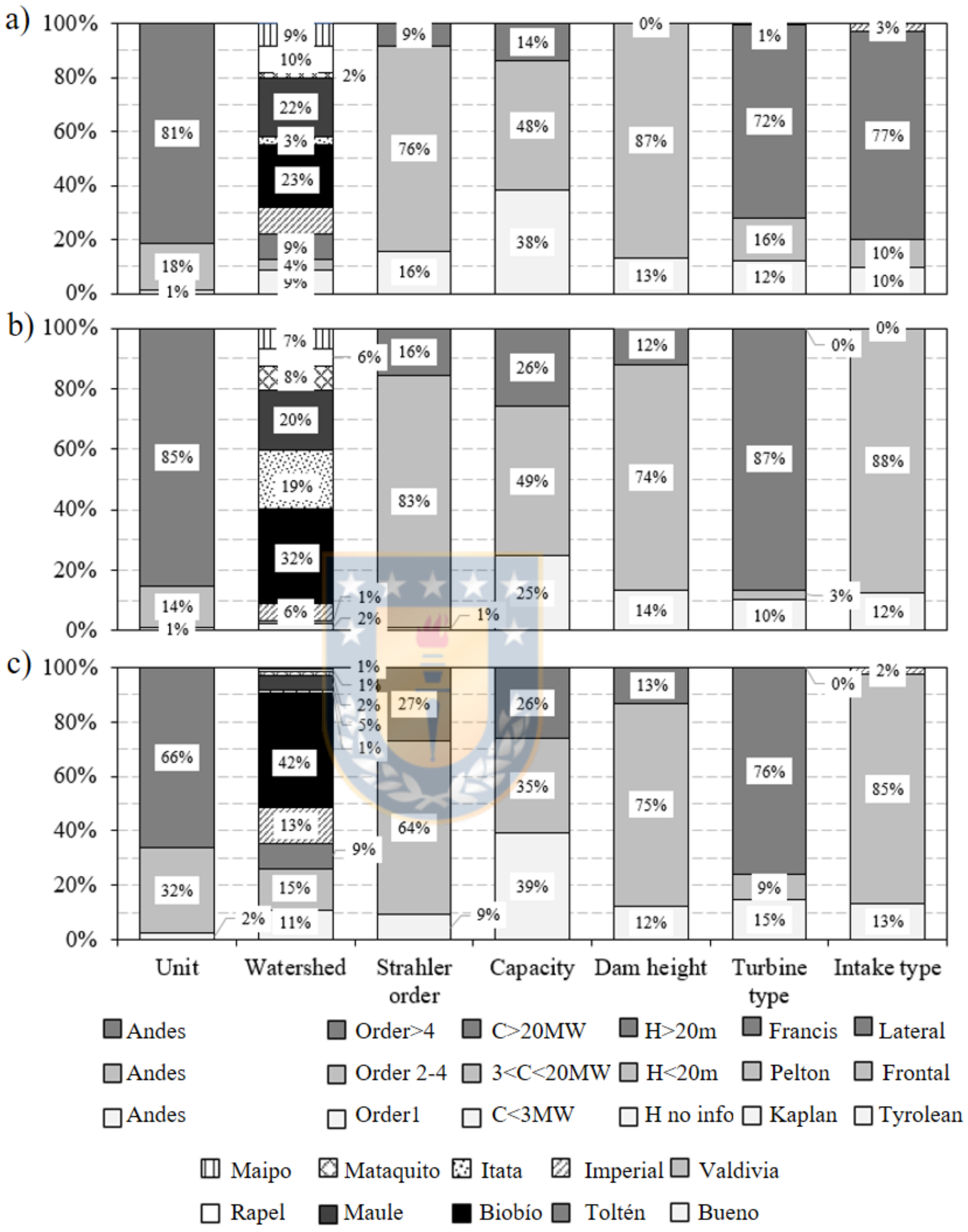


Figure 1-0-3. Characterisation (geographical unit, watershed, Strahler's order, capacity, dam height, turbine type, and water intake type) for projects.

Generalisation of results to projects with impassable barriers without fish data

Characteristics of the 219 sites with impassable barriers and fish data were compared to those of the 740 sites with impassable barriers and without fish data. The characteristics of these two project groups were similar (ANOSIM, R = 0.116, p = 0.001; Table 1- 2). Thus, we assume that our results were representative of all the planned hydropower projects in Central Chile.

Table 1-0-2. Hydropower project characteristics where fish are expected to be impacted, with and without fish data.

Character	**Projects with fish data (219) (%)**	**Projects without fish data (740) (%)**
Coastal plain	1.8	2.4
Central valley	24.2	11.9
Andean range	74.0	85.7
Strahler’s order 1	5.9	22.8
Strahler's order 2 to 4	71.7	75.1
Strahler’s order > 4	22.4	2.0
Capacity < 3MW	33.3	60.9
3 < Capacity < 20 MW	40.6	31.4
Capacity > 20 MW	26.0	7.7
Dam height < 20 m	74.4	92.2
Dam height > 20 m	12.8	2.2
Dam height unknown or no info	12.8	5.7
Kaplan turbine	12.8	16.2
Pelton turbine	6.8	22.3
Francis turbine	80.4	61.2
Turbine no info	0	0.3
Frontal intake	85.8	54.9
Tyrolean intake	12.8	35.8
Intake unknown	1.4	9.3

Statistical differences between site groups with different mitigation needs

Subgroups of project sites where mitigation is not required, where it is needed and considered feasible, and where it is needed but considered challenging were similar but presented some differences (ANOSIM, R_{global} = 0.165; p < 0.001).

Projects sites where mitigation is required and considered feasible or challenging were different (ANOSIM, $R_{pairwise}$ = 0.045; p = 0.005) and their differences were mainly explained by geographical unit (Andes: 85%, 66%; valley: 14%, 32%; coast: 1%, 2% – feasible and challenging solutions, respectively), and capacity (< 3 MW: 25%, 39%; 3-20 MW: 49%, 35%; > 20 MW: 26%, 26% – feasible and challenging solutions, respectively).

Project sites where mitigation is not required and where mitigation is required and considered challenging were similar with some differences (ANOSIM, $R_{pairwise}$ = 0.226; p = 0.001). Differences between these groups were predominantly explained by intake type (tyrolean intake: 10%, 13%; lateral intake with barrier: 10%, 85%; lateral intake without a barrier: 77%, 0%; no information: 3%, 2% – for no need of mitigation technology and for mitigation with a challenging solution, respectively), and geographical unit (Andes: 81%, 66%; Central Valley: 18%, 32%; Coast: 1%, 2% – for no need of mitigation technology and for mitigation with a challenging solution, respectively).

Finally, project sites where mitigation is not required and where mitigation is required and considered feasible were similar but with some differences (ANOSIM, $R_{paiwise}$ = 0.168; p = 0.001). Differences between these groups were mainly explained by intake type (tyrolean intake: 12%, 10%; lateral intake with barrier: 88%, 10%; lateral intake without a barrier: 0%, 77%; no information: 0%, 3% – for no need of mitigation technology and with a feasible solution, respectively), and basin (mainly in Itata: 3%, 19%; Biobío: 23%, 32%; Toltén river basin: 9%, 0% – for no need of mitigation technology and with a feasible solution, respectively) (Figure 1- 3).

Discussion

To conserve biodiversity within the constraints of limited resources, and to make management decisions in appropriate time-scales relative to the urgency of the threats and current rates of degradation of river environments, prioritisation of hydropower development should be made. In this study we aimed to develop a methodology to set conservation priorities for sustainable hydropower development by analysing the characteristics of native species and planned hydropower projects, that could be implemented in several different geographical zones, with different species distribution Hydropower projects where mitigation is not required were considered to produce only indirect impacts on native fish, mostly due to the possible alteration of the sedimentological regime and nutrients spiralling (Kemp, 2015). Other sources of impact such as injuries and mortality (e.g., blade strike, rapid pressure fluctuation, cavitation, shear stress and turbulence, Cada, 2001; Vowles et al., 2014) would need to be analysed on a case-by-case basis. Projects sites where mitigation is required and considered feasible allow the development of a standard solution, such as multi-species fishways, for the core group, as a starting point. A functional criterion based on habitat use was selected to identify the core group, as assemblages comprising the most prevalent genera occurring at planned project sites. Assuming that consent for the hydropower projects would be granted, the proposed strategy suggest that projects sites where mitigation is not required should be prioritised.

These projects total an installed capacity estimated to be 1,532 GW. Projects sites where mitigation is required and considered feasible should be contemplated if a mitigation technology is developed considering bounded requirements. These projects total an installed capacity estimated to be 3,904 GW. Consequently, these two subgroups of project sites (totalizing 15+35 = 50% of the planned projects, i.e., 5,437 GW) should be a prioritised considering they minimise the environmental impacts. The other projects considered challenging (50%) have the lowest priority, considering the need to develop a suitable site-specific mitigation solution.

As a result of the incentives of the Chilean Energy Policy that promotes that at least 70% of electricity generation should be from renewable sources by 2050 during the last decade the small hydropower sector increased in the Chilean energy matrix (Ministry of Energy, 2015; Arriagada et al., 2019) and many hydropower projects are planned for the near future. Until now, no hydropower projects have been built with a fishway provided.

There was no difference in the physical characteristics of sites where fish were expected, but this should be viewed with caution considering the absence of data in many cases. It could be assumed that the results obtained for sites with fish data are representative of the sites without. Consequently, in 35% of projects where fish species were predicted to be impacted, habitat fragmentation could be solved by means of a feasible mitigation technology (equivalent to 394 sites), and in 50% of them (equivalent to 565 sites), the mitigation technology would be challenging to achieve. A variety of devices have been installed at river barriers to restore connectivity as mitigation technology worldwide. The most common devices to assist displacements are fishways, structures that allow fish to swim upstream under their own effort (Clay, 1995). Mitigation technologies also include physical screens and surface bypasses, intended to prevent juveniles from passing through turbines (Larinier, 2001; Noatch and Suski, 2015). The extrapolation of the results to other projects without fish data based on the project characteristics was performed in an effort to estimate the magnitude of the challenge, and in an effort to overcome the scarcity of data which is common in neotropics. Caution must be taken when interpreting the results of such as an extrapolation, particularly when forming generalised conclusions related to the nature of impact on fish species. Consecutive studies should test this prediction. For any project, a developer should verify the basic information related to fish species present and the project characterisation, before deciding if mitigation technology recommended should be incorporated into the design.

Species with the greatest distribution along the river network or concentrated in the upper part of the rivers will be the most affected by future hydropower development in Chile as the potential is mainly concentrated in the Andean mountain range and in the Central Valley. Seven species do not overlap with any planned projects (*Cheirodon kiliani*, *D. chilensis*, *Brachygalaxias gothei*, *Mugil cephalus*, *Aplochiton marinus*, *Odontesthes brevianalis* and *O. itatanum*), and eight occur at more than 45 projects sites each (*T. areolatus*, *B.*

microlepidotus, *P. trucha*, *P. gillissi*, *P. irwini*, *G. maculatus*, *D. nahuelbutaensis* and *D. incognitus*). Of particular concern is the situation of *D. nahuelbutaensis*, *D. incognitus* and *P. irwini*, endemic to the study area, and present in at least in 49 projects sites. Moreover, although *B. microlepidotus*, *P. trucha* and *G. maculatus* were not part of the core group, they occurred in more than 67 projects sites. However, together these species would be impacted by only 13 projects and in other identified assemblages always co-occurred with different species. Thus, a solution for these assemblages needs to be developed on a case-by-case basis. At the watershed scale, the positive relationship between species richness and number of hydropower projects is also a cause for concern. This relation suggests that characteristics of the river networks that sustain greater biodiversity are also suitable for hydropower development.

The need to develop novel and innovative approaches for advancing Chilean native fish passage has been driven by the threat of a high pressure to develop hydropower (Habit et al., 2019). In Chile, efforts have been made by Laborde et al. (2016) and Link et al. (2017) to provide hydraulic design criteria for native species, while elsewhere others are also attempting to develop fishway design criteria that cater for a wider range of target species (Silva et al., 2012; Muraoka et al., 2017). In this study, a core group (comprising the TDP group, *Ch. pisciculus* and *B. maldonadoi*) has been identified as a starting point to advance fishway development for Chilean species exposed to hydropower projects. The core group was composed of small-bodied, benthic, nocturnal, benthofagous and resident species. In Chile, the genus *Trichomycterus* is represented by the widespread species *T. areolatus* and the endemic species *T. chiltoni*; *Percilia* by two endemic species, *P. irwini* and *P. gillissi*; and *Diplomystes* by four endemic species, *D. chilensis*, *D. incognitus*, *D. nahuelbutaensis* and *D. camposensis*. *Cheirodon pisciculus* and *B. maldonadoi* are also endemic. Within these groups, *B. maldonadoi* and all species of *Diplomystes* and *Percilia* have been classified as endangered. Solutions developed for the TDP group would likely be applicable to several other species of the same genera with similar biology (e.g., *T. aerolatus* and *T. chiltoni*, Pardo et al., 2005; *D. nahuelbutaensis*, *D. camposensis*, *D. incognitus* and *D. chilensis*, Beltrán-Concha et al., 2012; Arratia and Quezada-Romegialli, 2017).

Conclusion

The potential conflict associated with plans to exploit substantial hydropower potential and the requirement to protect unique native freshwater fish fauna emphasises the need for mitigation technologies, such as fishways.

Following the proposed strategic methodology to set priorities for sustainable hydropower development in a biodiversity hotspot, three categories of projects were identified according to their need for mitigation technology, namely project sites where mitigation is: (1) not required (15%), (2) required and considered feasible (35%), and (3) required but considered challenging (50%).

Further research on species characteristics belonging to the core group is needed to advance appropriate fishway technologies. Even when fishways have been recognised as half-way technologies (Kemp 2016), as their effectiveness can be low in many cases, the development of a fishpass for the identified core group of species would contribute to more sustainable hydropower development.

Acknowledgements

The financial support provided by the Chilean Research Council CONICYT through grant FONDECYT 1150154: ‘Within watershed barriers and among-watershed leaks: changing connectivity of rivers in central Chile and its impact on native fish is greatly acknowledged.

References

Arratia, G., Quezada-Romegialli, C., 2017. Understanding morphological variability in a taxonomic context in Chilean diplomystids (Teleostei: Siluriformes), including the description of a new species. *PeerJ*, 5, e2991.

Arriagada, P., Dieppois, B., Sidibe, M., Link, O. 2019. Impacts of climate change and climate variability on hydropower potential in data-scarce regions subjected to multi-decadal variability. Energies 12(14): 2747.

Branco, P., Amaral, S., Ferreira, M., Santos, J. 2017. Do small barriers affect the movement of freshwater fish by increasing residency?. Science of the Total Environment, 581, 486-494.

Beltrán-Concha, M., Muñoz-Ramírez, C., Ibarra, J., Habit, E., 2012. Análisis de la dieta de Diplomystes (Siluriformes: Diplomystidae) de Chile. Gayana, 76(2), 102-111.

Breder, C. 1926. The locomotion of fishes. Zoologica 4, 159–256.

Brown, J., Limburg, K., Waldman, J., Stephenson, K., Glenn, E., Juanes, F., Jordaan, A. 2013. Fish and hydropower on the US Atlantic coast: failed fisheries policies from half-way technologies. Conservation Letters, 6(4), 280-286.

Čada, G. 2001. The development of advanced hydroelectric turbines to improve fish passage survival. Fisheries, 26(9), 14-23.

Caro, T. 2010. Conservation by proxy: indicator, umbrella, keystone, flagship, and other surrogate species. Island Press.

Clarke, K., Gorley, R., 2015. Getting started with PRIMER v7. PRIMER-E: Plymouth, Plymouth Marine Laboratory.

Clay, C. 1995. Design of Fishways and Other Fish Facilities, Lewis Publishers. Ann Arbor, MI.

Díaz, G., Arriagada, P., Górski, K., Link, O., Karelovic, B., González, J., Habit, E. 2019. Fragmentation of Chilean Andean rivers: expected effects of hydropower development. Revista Chilena de Historia Natural, 91:1.

Dyer, B., 2000. Systematic review and biogeography of the freshwater fishes of Chile. Estud. Oceanol, 19, 77-98.

Fleishman, E., Murphy, D., Brussard, P. 2000. A new method for selection of umbrella species for conservation planning. Ecological applications, 10(2), 569-579.

Frankham, R. 2015. Genetic rescue of small inbred populations: Metaanalysis reveals large and consistent benefits of gene flow. Molecular Ecology, 24, 2610–2618.

Franklin, P., Bartles, B., 2012. Restoring connectivity for migratory native fish in a New Zealand stream: effectiveness of retrofitting a pipe culvert. Aquatic Conservation: Marine and Freshwater Ecosystems, 22(4), 489-497.

Franklin, P., Baker, C. 2016. Fish passage research in the Southern Hemisphere: Challenges, lessons and the need for novel solutions. In International Symposium on Ecohydraulics, Melbourne, Australia.

García, A., González, J., Habit, E., 2012. Caracterización del hábitat de peces nativos en el río San Pedro (cuenca del río Valdivia, Chile). Gayana, 76, 36-44.

Gibson, R., Headrich, R., Wernerheim, C., 2005. Loss of fish habitat as a consequence of inappropriately constructed stream crossings. Fisheries 30: 10–17.

Habit, E., Dyer, B., Vila, I. 2006. Current state of knowledge of freshwater fishes of Chile. Gayana, (1), 100-113.

Habit, E., García, A., Díaz, G., Arriagada, P., Link, O., Parra, O., Thoms, M. 2019. River science and management issues in Chile: hydropower development and native fish communities. River Research and Applications, 35(5), 489-499.

Habit, E., Victoriano, P., Campos, H., 2005. Ecología trófica y aspectos reproductivos de Trichomycterus areolatus (Pisces, Trichomycteridae) en ambientes lóticos artificiales. Revista de Biología Tropical, 53(1-2), 195-210.

Howell, P. 2006. Effects of wildfire and subsequent hydrologic events on fish distribution and abundance in tributaries of North Fork John Day River. North American Journal of Fisheries Management, 26, 983–994.

Jelks, H., Walsh, S., Burkhead, N., Contreras-Balderas, S., Diaz-Pardo, E., Hendrickson, D., Platania, S. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. Fisheries, 33(8), 372-407.

Kapitzke, I. 2010. Culvert fishway planning and design guidelines. Stage 1-Project Based Guidelines: Part E–Fish passage design site scale.

Katopodis, C., Gervais, R. 2012. Ecohydraulic analysis of fish fatigue data. River Research and Applications, 28(4), 444-456.

Kemp, P. 2015. Impoundments, barriers and abstractions: impact on fishes and fisheries, mitigation and future directions. Freshwater fisheries ecology, 717-769.

Kemp, P., 2016. Meta-analyses, Metrics and Motivation: Mixed Messages in the Fish Passage Debate. River Research and Applications, 32(10), 2116-2124.

Kumar, A., Schei, T., Ahenkorah, A., Caceres Rodriguez, R., Devernay, J. M., Freitas, M., Liu, Z. 2011. Hydropower. IPCC special report on renewable energy sources and climate change mitigation, 437-496.

Laborde, A., González, A., Sanhueza, C., Arriagada, P., Wilkes, M., Habit, E., Link, O. 2016. Hydropower Development, Riverine Connectivity, and Non-sport

Fish Species: criteria for Hydraulic Design of Fishways. River Research and Applications, 32(9), 1949-1957.

Lacey, R., Neary, V., Liao, J., Enders, E., Tritico, H. 2012. The IPOS framework: linking fish swimming performance in altered flows from laboratory experiments to rivers. River Research and Applications, 28(4), 429-443.

Larinier, M. 2001. Environmental issues, dams and fish migration. FAO fisheries technical paper, 419, 45-89.

Latrubesse, E., Arima, E., Dunne, T., Park, E., Baker, V., d'Horta, F., Ribas, C., 2017. Damming the rivers of the Amazon watershed. Nature, 546(7658), 363-369.

Lees, A., Peres, C., Fearnside, P., Schneider, M., Zuanon, J., 2016. Hydropower and the future of Amazonian biodiversity. Biodiversity and Conservation, 25(3), 451-466.

Liermann, C., Nilsson, C., Robertson, J., Ng, R., 2012. Implications of dam obstruction for global freshwater fish diversity. BioScience, 62, 539–548.

Link, O., Habit, E., 2015. Requirements and boundary conditions for fish passes of non-sport fish species based on Chilean experiences. Reviews in Environmental Science and Bio/Technology, 14(1), 9-21.

Link, O., Sanhueza, C., Arriagada, P., Brevis, W., Laborde, A., González, A., Habit, E. 2017. The fish Strouhal number as a criterion for hydraulic fishway design. Ecological Engineering, 103, 118-126.

McCluney, K., Poff, N., Palmer, M., Thorp, J., Poole, G., Williams, B., Baron, J. 2014. Riverine macrosystems ecology: sensitivity, resistance, and resilience of whole river basins with human alterations. Frontiers in Ecology and the Environment, 12(1), 48-58.

Meffe, G., Berra, T. 1988. Temporal characteristics of fish assemblage structure in an Ohio stream. Copeia, 684-691.

Ministry of Energy, 2015. Renewable energies in Chile: wind, solar and hydroelectric potential from Arica to Chiloé. Ministry of Energy and Dautsche Gesellschaft fur Internationale Zusammenarbeit. By Santana C., Falvey M., Ibarra M., y García M.

Ministry of Environment, 2015. Database of native ichthyofauna of Chile. Alejandra Figueroa. Requested to the Division of Natural Resources and Biodiversity.

MMA, 2018. http://www.mma.gob.cl/clasificacionespecies/ (Last accessed: 23/10/2018)

Muraoka, K., Nakanishi, S., Kayaba, Y. 2017. Boulder arrangement on a rocky ramp fishway based on the swimming behavior of fish. Limnologica, 62, 188-193.

Myers, N, Mittermeier, R., Mittermeier, C., Fonseca, G., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature, 403(6772): 853–858.

Noatch, M., Suski, C. 2012. Non-physical barriers to deter fish movements. Environmental Reviews, 20(1), 71-82.

Pardo, R., Scott, S., Vila, I., 2005. Shape analysis in Chilean species of Trichomycterus (Osteichthyes: Siluriformes) using geometric morphometry. Gayana, 69(1), 180-183.

Radinger, J., Wolker, C. 2014. Patterns and predictors of fish dispersal in rivers. Fish and Fisheries, 15, 456-473.

Romao, F., Quaresma, A., Branco, P., Santos, J., Amaral, S., Ferreira, M., Pinheiro, A. 2017. Passage performance of two cyprinids with different ecological traits in a fishway with distinct vertical slot configurations. Ecological Engineering, 105, 180-188.

Romao, F., Branco, P., Quaresma, A., Amaral, S., Pinheiro, A. 2018. Effectiveness of a multi-slot vertical slot fishway versus a standard vertical slot fishway for potamodromous cyprinids. Hydrobiologia, 816(1), 153-163.

Santos, J., Branco, P., Katopodis, C., Ferreira, T., Pinheiro, A. 2014. Retrofitting pool-and-weir fishways to improve passage performance of benthic fishes: effect of boulder density and fishway discharge. Ecological Engineering, 73, 335-344.

Sanz-Ronda, F., Ruiz-Legazpi, J., Bravo-Córdoba, F., Makrakis, S., Castro-Santos, T. 2015. Sprinting performance of two Iberian fish: Luciobarbus bocagei and Pseudochondrostoma duriense in an open channel flume. Ecological Engineering, 83, 61-70.

Sfakiotakis M, Lane D., Davies J. 1999. Review of fish swimming modes for aquatic locomotion. Journal of Oceanic Engineering, 24(2):237–252.

Silva, A., Katopodis, C., Santos, J., Ferreira, M., Pinheiro, A. 2012. Cyprinid swimming behaviour in response to turbulent flow. Ecological Engineering, 44, 314-328.

Small Hydropower World, 2013. World Small Hydropower Development Report. United Nations Industrial Development Organization (UNIDO), Vienna.

Stephens, P., Sutherland, W. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends in Ecology & Evolution, 14, 401–405.

Thornton, D., Zeller, K., Rondinini, C., Boitani, L., Crooks, K., Burdett, C., Quigley, H. 2016. Assessing the umbrella value of a range-wide conservation network for jaguars (Panthera onca). Ecological Applications, 26(4), 1112-1124.

Valenzuela-Aguayo, F., McCracken, G., Manosalva, A., Habit, E., Ruzzante, D. 2019. Human-induced habitat fragmentation effects on connectivity, diversity and population persistence of an endemic fish, Percilia irwini, in the Biobío river basin (Chile). Evolutionary Applications.

Vila, I., Contreras, M., 1999. Peces límnicos de Chile. Boletín del Museo Nacional de Historia Natural. Chile, 48, 61-75.

Vila, I., Habit, E. 2015. Current situation of the fish fauna in the Mediterranean region of Andean river systems in Chile. FISHMED Fishes Mediterr Environment, 2(19).

Vörösmarty, C., McIntyre, P., Gessner, M., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S., Sullivan, C., Liermann, C., Davies, P., 2010. Global threats to human water security and river biodiversity. Nature, 467, 555–561.

Vowles, A., Karlsson, S., Uzunova, E., and Kemp, P. 2014. The importance of behaviour in predicting the impact of a novel small-scale hydropower device on the survival of downstream moving fish. Ecological engineering, 69, 151-159.

Warwick, R., and Clarke, K., 1998. Taxonomic distinctness and environmental assessment. Journal of Applied ecology, 35(4), 532-543.

Wilkes M, Webb A, Pompeu P, Silva L, Baker C, Franklin P, Link O, Habit E, Kemp P, Vowles A. 2019. Not just a migration problem: metapopulations, habitat shifts and gene flow are also important for fishway science and management. River Research and Applications.

Winemiller, K. O., McIntyre, P. B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., Stiassny, M., 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. Science, 351(6269), 128-129.

Zarfl, C., Lumson, A., Berlekamp, J., Tydecks, L., Tockner, K., 2015. A global boom in hydropower dam construction. Aquatic Sciences, 77(1), 161-170.

Zhou, Y., Hejazi, M., Smith, S., Edmonds, J., Li, H., Clarke, L., Thomson, A., 2015. A comprehensive view of global potential for hydro-generated electricity. Energy and Environmental Science, 8(9), 2622-2633.

Ziv, G., Baran, E., Nam, S., Rodríguez-Iturbe, I., Levin, S. 2012. Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin. Proceedings of the National Academy of Sciences, 109(15), 5609-5614.

CHAPTER 2: FINDING SHARED NEEDS: FISHWAY DESIGN CRITERIA FOR A SMALL-BODIED TARGET GROUP

This chapter is based on:

Laborde, A. (in preparation)

Finding shared needs: fishway design criteria for a small-bodied target group.

Finding shared needs: fishway design criteria for a small-bodied target group

A. Laborde[a]

[a] *Department of Aquatic Systems, Faculty of Environmental Sciences and EULA Centre, Universidad de Concepción, Concepción, Chile*

Abstract

Significant efforts have been made to reconnect freshwater systems to facilitate fish movement through the design and installation of dedicated fishway structures. An understanding of swimming performance is crucial for the effective design of fishway mitigation technologies, making sure that the water velocities within them do not exceed the swimming capacities of fish species. Nevertheless, without reference to other biological criteria, the use of critical swimming velocity and endurance for fishway design rests on assumptions regarding swimming performance. This study aimed to estimate swimming performance for *Trichomycterus areolatus*, *Percilia irwini* and *Diplomystes nahuelbutaensis* (the TDP group), a small-bodied target group identified as a priority for fishway development in Chile. The review highlights (1) the importance of TDP group conservation as a small-bodied target group; (2) estimation of the swimming performance of TDP group species based on applicability of generalised dimensionless variables proposed by Katopodis and Gervais (2016) and a correlation of swimming capacities with fish species characteristics proposed by Watson et al. (2019); (3) estimation of the maximum suitable fishway length for the TDP group; and (4) the need to develop fish passage experiments for small-bodied fish. Finally, the relevance and limitations of small-bodied swimming performance data in fishway design is also discussed. Taxonomic orders comprising both large-bodied and small-bodied fish species are few (e.g., Perciform, Siluriform, Osmeriform and Galaxiids). Nevertheless, large-bodied and small-bodied fish species of the same taxonomic order have been shown to be adimensionally incomparable. Results suggest that, for fish species of the same taxonomic order, small-bodied fish species exhibit higher endurance than large-bodied fish in dimensionless terms. Furthermore, the main results show that small-bodied fish species are internally comparable, validating the application of dimensionless variables between small-bodied fish species. Based on results obtained by Watson et al. (2019) in the form of dimensionless endurance curves of Perciform small-bodied fish species, a reliable source of expected swimming performance was derived for other small-bodied fish of the same taxonomic order. This finding emphasised the need for robust swimming performance information for small-bodied fish. Furthermore, to continue advancing in the development of technologies to mitigate the impact of instream structures on small-bodied fish species, continued research is necessary on small-bodied fish behaviour and its interaction with complex fishway hydraulics. Passage effectiveness and space use in small-bodied fishway design should be tested.

Keywords: Fish passage, conservation, mitigation, multi-species, small-bodied fish, Chile.

Introduction

Understanding fish movement between habitats is important, not only as a key trait for fish population management and conservation monitoring (Vivanco et al., 2021), but also for their role in the wider ecosystem (Knapp et al., 2019). Structures within and along rivers often impede the displacement of fish species up and down rivers. Significant efforts have been made to develop and refine fish passage facilities to facilitate both discharge and fish passage. Dedicated fishways have been developed for highly prevalent or economically important species in the Northern Hemisphere in particular (Noonan et al., 2012). However, research findings for these species and the resulting remediation solutions do not necessarily extrapolate to other species (Birnie-Gauvin et al., 2018; Goodrich et al., 2018; Silva et al., 2018). This is particularly true for small-bodied fish, a term that refers to adult fish with a body length of up to 15 cm. Small-bodied fish are present around the world; however, they are mostly native and endemic to regions of the southern temperate zone, particularly Australia (Watson et al., 2019), New Zealand (Magaju et al., 2020), southern South America (Link et al., 2017; Laborde et al., 2016; Link and Habit, 2015) and Southern Africa (Boubeé et al., 1999; Cussac et al., 2009). A significant lack of systematic, distributional, biological and ecological information for these species has frequently been noted (e.g., Laborde et al., 2016; Franklin and Gee, 2019). This lack of knowledge to inform the design of fishways that enable unimpeded displacement of small-bodied fish or species which, at the juvenile stage, have a body length of up to 15 cm, is compounded by the pressure exerted by rapid economic expansion and land development (Wilkes et al., 2017; Habit et al., 2018). In this context, rivers are harnessed and modified, with significant effects on the ecosystem (Knapp et al., 2019).

The South-Central region of Chile has been generating considerable attention in terms of hydropower exploitation, as it comprises 10 high gradient watersheds with an estimated 12.5 GW potential (Ministry of Energy, 2015), most of which would be supplied by small hydropower plants (SHPs). Central Chile is also part of the Chilean ichthyogeographic province (*sensu* Dyer, 2000), a biodiversity hotspot (Myers et al., 2000) accommodating a unique and highly endemic fish fauna. Thus, of major concern are the potential fragmentation of the entire region and the cumulative effects of multiple projects built within the natural range of native species that are predominantly small-bodied and resident (Díaz et al., 2019). This background highlights the need to develop effective bi-directional fishways for small-bodied Chilean native fish species or species which, at the juvenile stage, have a body length of up to 15 cm. However, advances in technology and design must be accelerated if fish populations such as small-bodied Chilean native species are to endure. In order to establish priorities for the development of effective mitigation technology targeting native assemblages in Chile, an ecoregion with high endemism, Laborde et al. (2020) developed a methodology to prioritise assemblages comprising the most prevalent genera occurring at planned project sites. *Trichomycterus*, *Diplomystes* and *Percilia* (the

TDP group) were the three genera of small-bodied fish species identified as a starting point. However, there are important gaps in knowledge concerning these freshwater fish (Habit et al., 2006; Vila et al., 2006). In Chile, efforts have been made by Laborde et al. (2016) and Link et al. (2017) to provide hydraulic design criteria for native species. Laborde et al. (2016) characterised endurance curves for two small-bodied Chilean native species. Results showed that *Cheirodon galusdae* and juveniles of *Basilichthys microlepidotus* were capable of very similar critical velocities of 69.7 and 69.6 cm/s^{-1}. Based on their results, fishway design curves were proposed for both species. Link et al. (2017) found that the same fish species tested by Laborde et al. (2016) exhibited markedly different swimming styles when confronted with a von Kármán vortex street. While one species managed to partially adapt its swimming gait to the ensuing regular vortex street, thus maintaining stability, the second species was repeatedly destabilised by the turbulence. Other researchers are also attempting to develop fishway design criteria that cater to a wider range of target species (Silva et al., 2012; Muraoka et al., 2017).

The effective design of fishway mitigation technologies is informed by ecohydraulics, integrating factors both physical (hydrology, hydraulics and habitat morphodynamics) and biological (life cycle requirements, migration behaviour and fish swimming performance, including capability, metabolism and kinematics) (Haefner and Bowen, 2001; Katopodis, 2005; Noonan et al., 2012; Braaten et al., 2015). Key parameters are related to swimming modes (Brett, 1967; Sfakiotakis et al., 1999), endurance (Beamish, 1978; Brett, 1964), turbulence effects (Lacey et al., 2012; Liao, 2007; Lupandin, 2005; Nikora et al., 2003) and behaviour (Plew et al., 2007; Russon and Kemp, 2011).

Swimming performance is one of the most important features that mediate fish fitness and survival (Tudorache et al., 2008; Jones et al., 1974; Burgess et al., 2006). It plays a crucial role in dispersal, migration, habitat selection, predator-prey interactions and reproduction (Kolok, 1999; Reidy et al, 2000; Videler, 1993). Fish swimming performance is traditionally assessed using swim tunnels and ecohydraulic flumes (Videler et al., 1993; Katopodis et al., 2019). To measure swimming performance, individual fish are forced to swim against water flow of increasing velocity until fatigue, that is, the moment at which the fish can no longer swim and maintain its position in the current (Beecham et al., 2009). The most widely accepted and commonly applied works on the subject are those of Beamish (1966) and Brett (1964). Beamish (1966) states that fish swimming performance can be classified into three categories: sustained, prolonged and burst swimming. Sustained swimming is aerobically fuelled and can be maintained for long time periods, typically more than 200 min, without muscular fatigue (Brett, 1967; Beamish, 1966; Hoover et al., 2017). The maximum swimming velocity of which fish are capable is burst swimming, which can be maintained only for shorter periods (typically < 20–30 s) and is fuelled anaerobically (Beamish, 1978; Hoover et al., 2017). Prolonged swimming is the transitional mode between sustained and burst swimming and is barely distinguishable from burst swimming in some species (Hoover et al., 2017). Prolonged swimming is fuelled by both aerobic and anaerobic metabolism, and can be maintained for intermediate intervals of time (1–200 min) (Beamish, 1966; Hoover et al., 2017). Brett (1964) analyses how the metabolic rate of salmon varies with its swimming velocity, its size, and water temperature. Metabolic rate increases with temperature, while in terms of velocity, the author identifies a metabolic threshold above which oxygen debt begins to apply. In terms of size, larger individuals have lower metabolic consumption (they are more efficient) than smaller individuals at low velocities, but this gap narrows as velocity increases. Many authors have opted to determine critical swimming velocity (*U*crit) as a measurement of prolonged swimming performance, even measuring oxygen consumption rates at the same time (Hammer, 1995). However, this methodology presents disadvantages regarding fish that do not exhibit rheotactic behaviour and do not swim in the water column. A variety of approaches have been proposed as a result. For example, Haro et al. (2004) quantify responses to four constant test conditions in a flume model by means of a passive integrated transponder (PIT) system installed every 5 m. Although the fish have sufficient space to deploy their swimming strategies, the distance between antennae could be too large, producing an error factor in estimation of swimming performance. Peake (2008) uses changes in tail beat velocity to identify different swimming categories, which could be biased towards a specific swimming strategy. Vezza et al. (2020) propose a methodology targeting bottom-dwelling fish that focuses on their burst-and-coast swimming style, but does not take into consideration periods of coasting. However, the authors did not find any meaningful differences between the two calculation methods. Recently, Cano-Barbacil et al. (2020) reviewed the key factors explaining critical swimming velocity for Iberian species, finding that body length is largely the most important predictor of critical velocity, followed by family, time step interval and species identity. By contrast, the less important variables were form factor, temperature, body shape and native status. Moreover, burst velocity is also important for fishway design because fish often use this velocity to bypass objects, high-velocity zones, turbulence and eddies within fishways (Pavlov, 1989; Katopodis, 2005; Cocherell et al., 2011; Silva et al., 2012; Sanz-Ronda et al., 2015; Quaranta et al., 2017; Wang and Chanson, 2018). Although a number of internal and external factors (e.g., population and body size, season and temperature, sex, water quality, light, and food availability) affect swimming performance, making the intraspecific and interspecific comparison complex (McKenzie et al., 2001; Geist et al., 2005; Allen et al., 2006).

Fishway mitigation technologies for large-bodied species (often known as sport species, e.g., salmon) are based on extensive ecohydraulic research, while design of fishways for small-bodied fish species frequently relis on limited biological information (Katopodis, 2005). Nevertheless, in the absence of other biological criteria, the use of critical swimming velocity or endurance for fishway design rests on assumptions regarding swimming performance. Lessons learned over time and knowledge accrued from comprehensive studies have improved understanding, providing instructive paradigms and offering optimism for reconnecting small-bodied habitats (Jager et al., 2016; Katopodis and Williams, 2016). In fishway design, it is common to use endurance curves to gather specific information on how long (endurance times) and how far (swimming distances) a particular fish can swim against given water velocities (Katopodis, 1992). Katopodis (1994) proposed velocity and time-dimensionless variables to generalise data. Katopodis and Gervais (2016) created a swimming performance database for 131 fish species using data extracted from the literature (mainly large-bodied fish species). Their results showed significant correlations for all species as a single group, and the statistics allowed improved separation of species into groups. Curves were therefore defined by taxonomic order and family (such as Percidae, Moronidae, Ictaluridae and Osmeridae) and by swimming mode (i.e., anguilliform, subcarangiform, carangiform and a combination of swimming modes). Killen et al. (2016) identified taxonomic family as a good predictor of critical velocity despite marked differences in lifestyle and form among species within the same family. These differences in swimming capacity might be related to differences in their habitat preferences (Cano-Barbacil et al., 2020). Watson et al. (2019) tested swimming capacities of Australian small-bodied fish. Their results showed that body length combined with depth station (benthic, pelagic or surface) explained most of the interspecific variation in the small-bodied fish swimming performance data observed. Fish length alone proved to be a robust characteristic for predicting a fish’s swimming capability. Using only fish length, predicted critical velocity values were very similar to that observed for each species (Watson et al., 2019). Individual addition of body shape, tail shape or depth station as co-predictors yielded an overall improvement to the predicted critical velocity values (all p = 1, meaning predicted values were overall very similar to the observed data; Watson et al., 2019). Finally, Peake (1997) proposed design curves that define the maximum distance that fish can swim through a fishway, based on the flow velocity, the fish swimming velocity, and the time that they can maintain said swimming velocity (defined by the endurance curve). The present study aimed to estimate swimming performance for a small-bodied target group – the TDP group – identified as a priority for fishway development in Chile. Swimming capacities were estimated based on information collected from the literature: applicability of proposed dimensionless variables, and a proposed correlation of swimming capacities with fish species characteristics. First, the available information on swimming abilities for the genera present in the TDP group was reviewed, considering large-bodied and small-bodied fish species. Then, the applicability of the generalised curves proposed by Katopodis and Gervais (2016) for small-bodied species was analysed. Then, the species with similar characteristics to the species present in the TDP group were reviewed. Swimming capacities for *T. areolatus*, *P. irwini* and *D. nahuelbutaensis* were estimated based on previous results and according to the hypotheses of Katopodis and Gervais (2016) and Watson et al. (2019). Results are discussed in terms of applicability to both the TDP group and other small-bodied fish species.

Finally, based on estimated swimming performance and body length range, the expected distance design curve as proposed by Peake (1997) was calculated. The relevance and limitations of swimming performance data for small-bodied fish in fishway design is also discussed.

Trichomycterus, Diplomystes **and** ***Percilia*** **Swimming Performance**

Trichomycterus, *Diplomystes* and *Percilia* (the TDP group) were the most frequent genera in the assemblages present at planned hydropower projects sites in South Central Chile (i.e., present at 40% of sites; Laborde et al., 2020). The TDP group is composed of two small-bodied fish species (*T. areolatus* and *P. irwini*) and a species that coexists alongside them in its juvenile stage (*D. nahuelbutaensis*, juveniles up to 15 cm; Arratia et al., 1983). All three are benthofagous and resident species. *Trichomycterus* and *Diplomystes* belong to the Siluriformes, while *Percilia* belong to the Perciforms. *Trichomycterus* is represented in Chile by the widespread species *T. areolatus* and by the species *T. chiltoni*, which is endemic to Chile; *Percilia* by two endemic species: *P. irwini* and *P. gillissi*; and *Diplomystes* by four endemic species: *D. chilensis*, *D. incognitus*, *D. nahuelbutaensis* and *D. camposensis*. All of these species are distributed between the Aconcagua River (32° Lat S) and the Bueno River (41° Lat S) basins. Based on Breder's classification (1926), species of the genus *Trichomycterus* exhibit an anguilliform swimming mode, while *Percilia* and

Diplomystes present a subcarangiform swimming mode. In terms of conservation status, *Trichomycterus* spp., *Percilia* spp and *Diplomystes* spp. are classified as Endangered (Ministry of Environment, 2018). Sexual maturity for *P. irwini*, *T. areolatus and D. nahuelbutaensis* is around 5.5 cm (Garcia et al., 2012), 5.5 cm (Manriquez et al., 1988), 11 cm (Vila et al., 1996; Beltrán-Concha et al., 2012), respectively.

Maximum body size (total length) for *P. irwini* and *T. areolatus* is around 9 cm (Valenzuela et al., 2020; Vivanco et al., 2021) and 12.0 cm, respectively. For *D. nahuelbutaensis*, only juvenile individuals were analysed (up to 15 cm).

P. irwini inhabit rithral to potamal zones along rivers (García et al. 2012; Habit and Belk 2007) and have a maximum reported migration rate of 26 km in 4 months in the downstream direction. *T. areolatus* inhabit rithral to transitional zones in areas with coarse substrate and slow to medium current velocity. Juveniles inhabit currents of less than 0.5 m/s^{-1} and adults less than 0.9 m/s^{-1} (Arratia, 1983; Penaluna et al., 2009; Scott et al., 2007). *D. nahuelbutaensis* inhabit rithral zones with coarse substrate, high turbulence, high dissolved oxygen and low temperature. Juveniles inhabit currents of less than 0.5 m/s^{-1} and adults less than 1.64 m/s^{-1} (Arratia, 1983, 1987). They have a maximum migration rate of 3 km in 53 days in the downstream direction (Penaluna et al., 2009)

Research Methods

Genera swimming performance review

A review was conducted of the literature on the swimming performance of small-bodied fish species. In addition, swimming performance information was reviewed specifically for the genera *Percilia*, *Trichomycterus* and *Diplomystes*, covering both large-bodied and small-bodied fish species. If the information was not available at the genus scale, the search continued at the family scale and, finally, taxonomic order.

Swimming performance

Katopodis (1994) hypothesises that similar species (i.e., by taxonomic order and family) often present similar swimming performance, meaning that species are well-represented by the same endurance curve.

To test this hypothesis, the dimensionless curves proposed by Katopodis and Gervais (2016), estimated based on their entire database of fish (mainly large-bodied), were compared with the reviewed small-bodied fish database. Furthermore, for the same taxonomic order, information on large-bodied and small-bodied fish species was compared, and analysis was conducted to identify similarities in the behavioural trends of the two sizes.

The endurance curve is described by the following dimensionless variables: fish velocity ($U^* = U \times (g \times L)^{-1/2}$, where U is flow velocity (m/s), L is fish body length (m) and g is gravitational acceleration (9.81 m/s^2)); and time ($t^* = t \times (L/g)^{-1/2}$, where t is time to fatigue (s)). Considering that fish swimming velocity generally scales with the square root of fish length, similar to exponential decay curves, Katopodis and Gervais (2016) proposed dimensionless endurance curves ($U^* = K (t^*)^b$, where K is sustained endurance (without fatigue) and b is endurance decay rate) based on their swimming performance database of 131 fish species and data for over 27,000 fish, mainly large-bodied.

Cano-Barbacil et al. (2020) reviewed the key factors explaining critical swimming velocity for Iberian species, finding that body length is largely the most important predictor of critical velocity, followed by family, time step interval and species identity. Watson et al. (2019) found that body length combined with depth station (benthic, pelagic or surface) explained most of the interspecific variation in observed small-bodied fish swimming performance data. Consequently, body length, depth station and habitat of *T. areolatus*, *P. irwini* and *D. nahuelbutaensis* were characterised and compared to available information pertaining to swimming performance of small-bodied fish species within the same taxonomic order.

Finally, based on the reliability of dimensionless endurance curves proposed by Katopodis and Gervais (2016) and on the small-bodied fish database and information available on fish relating to the TDP group provided by Watson et al. (2019), expected swimming performance for the TDP group was estimated.

Reported information concerning small-bodied kinematics was also reviewed to highlight expected fish behaviour.

Predicting swimming distances

Design curves defining maximum suitable fishway lengths were proposed by Peake et al. (1997). The proposed curves for allowable fishway lengths are defined as U = Us – (D/t), where U is flow velocity (m/s), Us is fish swimming velocity (m/s), t is endurance time at Us, and D is fishway length. Consequently, proposed distance curves and maximum allowable fishway length for the TDP group were estimated based on predicted swimming performance.

Swimming performance literature review

Fish body length is a key biological factor to understanding swimming performance (Plaut, 2001; Katopodis and Gervais, 2016; Beamish, 1978; Katopodis and Gervais, 2012). It is well known that absolute critical swimming velocity (*U*crit expressed in cm/s^{-1}) scales with fish body length (Mateus et al., 2008) as described in earlier studies of sustained and prolonged swimming. Besides body length, it is important to note that body mass may also be a key predictor of *U*crit, especially when it comes to comparing swimming abilities among species with different body shapes and swimming and propulsion types

(Videler et al., 1993; Beamish 1978, Rubio-Gracia et al., 2020). Body mass is directly related to body volume and, therefore, to the energy expenditure needed to move against the flow (Ohlberger et al., 2005; Srean et al., 2016). Moreover, energy costs of swimming (i.e., the amount of energy needed to transport one unit of body mass per unit of distance) are negatively associated with body mass because of the lower surface area to volume ratio of larger fish (Webb, 1975; Schmidt-Nielsen, 1972). Thus, the surface in contact with water per unit of volume is larger in small fish, increasing the friction drag and the relative dissipated energy (Sfakiotakis, 1999). In addition, there is a direct association between body volume and muscle mass and the number of myofilaments, which favour swimming performance (Hammer, 1995). As expected, body shape significantly influenced fish swimming performance. Earlier studies showed that body shape also influences the energetic costs associated with swimming (Ohlberger et al., 2005; Rubio-Gracia et al., 2020). In general, streamlined fish tend to maximise thrust while minimising drag and recoil energy losses (Webb, 1975; Langerhans and Reznick, 2010). Correspondingly, fish evolve body forms that enhance steady swimming (i.e., swimming at constant velocity in a straight line) in open-water habitats, high-flow environments, and areas with relatively high competition for patchily-distributed resources (Langerhans and Reznick, 2010). Steady swimming is generally enhanced with a streamlined body shape, a shallow caudal region and a high aspect ratio of the caudal fin (Froese, 2006; Weihs, 1973). Results obtained by Cano-Barbacil et al. (2020) showed that elongated and fusiform body shapes are better adapted to swimming steadily. On the other hand, species that present the opposite suite of morphological traits, such as eel-like and short and deep bodies, tend to optimise unsteady swimming (i.e., more complicated locomotor patterns in which changes in velocity or direction occur, such as fast-starts, rapid turns, braking, and burst-and-coast swimming; Webb, 1984). Burst-and-coast swimming consists of alternating phases of active swimming and gliding and is used by fish to reduce power expenditure when swimming at high constant velocities (Kern et al., 2018; Tudorache et al., 2007; Wu et al., 2007). Moreover, other species adapted to a specific environment, such as bottom-dwelling or flatfish species, usually perform poorly in *U*crit (Tudorache et al., 2008; Knaepkens et al, 2007; Duthie et al., 1982). Consistent with these earlier findings, results presented by Cano et al. (2020) also indicated that benthic and flatfish species have relatively lower *U*crit.

In addition, the effect of temperature on *U*crit is also one of the most important abiotic factors influencing fish swimming performance (Webb, 1975; Fry, 1947; 1971; Brett, 1971). Specifically, the relationship between *U*crit and temperature is commonly described by a bell-shaped curve (Randal and Brauner, 1991). Mechanistically, this can be explained by a general decline in all physiological processes at low temperatures (e.g., a decrease in power generated by the muscle) that also reduces *U*crit (Mckenzie and Claireaux, 2010). As temperature increases, there is a positive effect on muscle functioning, and its associated power generation contributes to an increase in swimming performance

(Jhonston and Temple, 2002; Rome, 2007). Nevertheless, when temperature exceeds the optimum range, the oxygen-carrying capacity of the blood decreases and restrains oxygen delivery to the tissues (Randal and Brauner, 1991).

In an attempt to remedy the lack of information concerning small-bodied fish, we conducted a review of the literature on swimming performance of small-bodied fish species. Laborde et al. (2016) characterised endurance curves for two small-bodied Chilean native species. Results showed that *Cheirodon galusdae* and juveniles of *Basilichthys microlepidotus* were capable of very similar critical velocities of 69.7 and 69.6 cm/s^{-1}. Based on this, fishway design curves were proposed for both species. Link et al. (2017) found that the same fish species tested by Laborde et al. (2016) exhibited distinctly different swimming styles when confronted with a von Kármán vortex street. While one species managed to partially adapt its swimming gait to the ensuing regular vortex street, thus maintaining stability, the second species was repeatedly destabilised by the turbulence. Watson et al. (2019) report the swimming performance capacities of 21 small-bodied fish and juveniles (< 10 cm) of large-bodied species native to Australia as measured by critical swimming velocity (*U*crit) and burst swimming velocity (*U*sprint) in a recirculating flume. This data is complemented by endurance swim trials conducted in a 12-metre hydraulic flume channel. Building on the utility of this dataset, we used a panel of morphological, behavioural and ecological traits first to assess their relative contributions to the observed swimming performance data, and second to determine whether they could be used to predict swimming performance capacity. Dupont (2020) assessed swimming performance of four New Zealand native species (Redfin bully *Gobiomorphus huttoni*, Inanga *Galaxias maculatus*, Banded Kōkopu *Galaxias fasciatus* and Common Smelt R*etropinna retropinna)* using a Steffensen-type swim tunnel produced by Loligo Systems (model SW10050). Water temperature was 14.5°C (± 1°C) with 82% dissolved oxygen. The individual performance of fish was recorded and calculated using the critical swimming velocity (*U*crit) for active swimmer fish and using the sprint swimming velocity (*U*sprint) for benthic species. Sampaio et al. (2020) analysed and compared the critical swimming velocitys of four trichomycterid fish species from epigean and hypogean environments: *Trichomycterus itacarambiensis* and *Ituglanis passensis*, both troglobitic from underground rivers; *Trichomycterus brasiliensis* from epigean rivers; and *Ituglanis sp.*, an undescribed troglophile species from an underground stream. Swimming tests were conducted with a non-volitional apparatus in which fish swim against a progressive incremental water velocity until they could no longer resist the flow.

Information was not available for any of the genera. For *Percilia* and *Trichomycterus*, information was obtained for their families: Percidae and Trichomycteridae. For *Diplomystes*, information was obtained for the order Siluriformes. A summary of similar species (i.e., by family or taxonomic order) with the available information is shown in Table 2-1.

Table 2-1. Summary of species similar to *Trichomycterus*, *Percilia* and *Diplomystes* with their available information (i.e., critical velocity and/or endurance), taxonomic characterisation, body size and source of information.

Similar to	**Order**	**Family**	**Scientific name**	**Available information**	**Body size**	**Reference**
Percilia irwini	Perciform	Percichthyidae	*Nannoperca australis*	Critical velocity and endurance	Small-bodied	Watson et al. (2019)
	Perciform	Percichthyidae	*Macculochella peeli*	Critical velocity and endurance	Large-bodied	
	Perciform	Percichthyidae	*Macquaria novemaculeata*	Critical velocity and endurance	Large-bodied	
	Perciform	Percichthyidae	*Macquaria ambigua*	Critical velocity and endurance	Large-bodied	
	Perciform	Percidae	*Perca flavescens*	Critical velocity and endurance	Large-bodied	Katopodis and Gervais (2016)
Trichomycterus areolatus	Siluriform	Trichomycteridae	*Trichomycterus itacarambiensis*	Critical velocity	Small-bodied	Sampio et al. (2020)
	Siluriform	Trichomycteridae	*Trichomycterus brasiliensis*	Critical velocity	Small-bodied	
	Siluriform	Trichomycteridae	*Itunglanis passensis*	Critical velocity	Small-bodied	
	Siluriform	Trichomycteridae	*Itunglanis sp*	Critical velocity	Small-bodied	
Diplomystes nahuelbutaensis	Siluriform	Ictaluridae	*Ictalarus punctatus*	Endurance	Large-bodied	Beecham (2007; 2009); Leavy and Bonner (2009)
	Siluriform	Ictaluridae	*Ictalarus furcatus*	Endurance	Large-bodied	

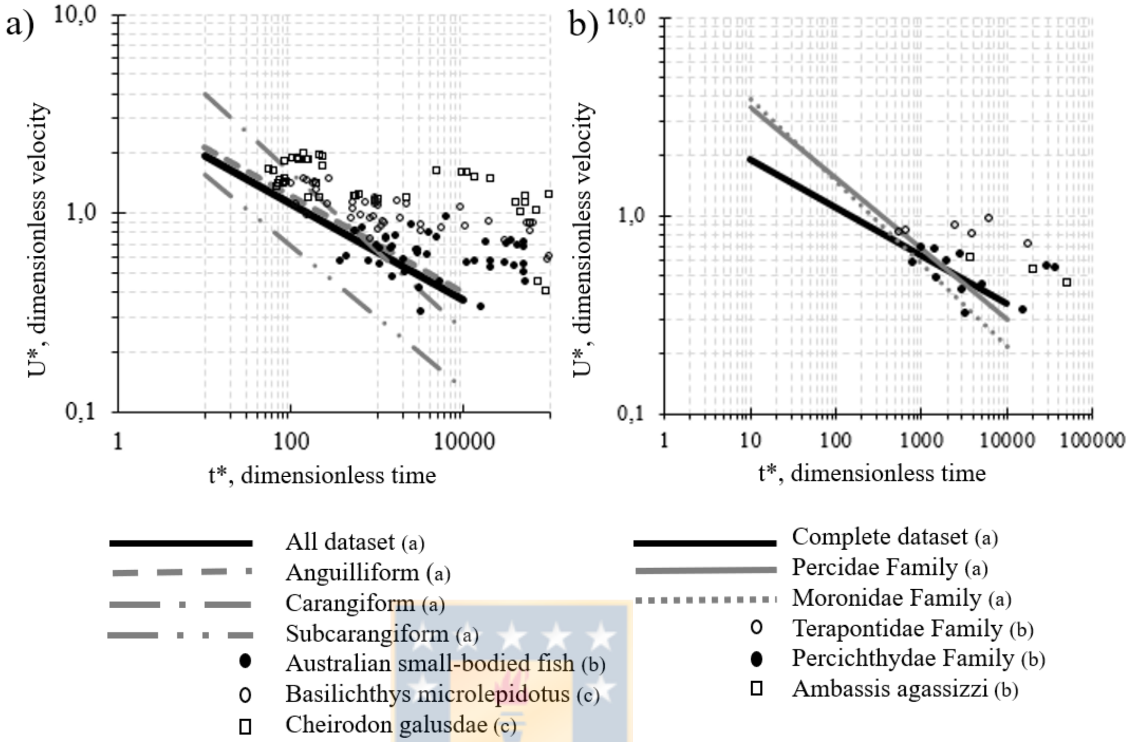
Swimming performance based on fish database generalisation

To test Katopodis and Gervais (2016) hypothesis, the reviewed fish database was compared with the generalised database for the same taxonomic families and small-bodied and large-bodied species.

Table 2-2. Dimensionless endurance curves (i.e., fish swimming velocity versus dimensionless time-to-fatigue) for all data, classified by swimming mode. Percidae and Moronidae families, both belonging to the Perciform order, are also presented (according to Katopodis and Gervais, 2016).

Dataset	**A**	**b**	**K**	**R²**	**n**
All processed data	1,217	-0,242	3,377	0,598	22506
Swimming mode: Angulliform	1,269	-0,359	3.557	0,844	1747
Swimming mode: Carangiform	229	-0,396	9876	0,905	592
Swimming mode: Subcarangiform	1324	-0,243	3757	0,695	18044
Percidae family	2,072	-0,356	7941	0,861	372
Moronidae family	2,321	-0,418	10,189	0,987	285

Fig. 2-1 shows the comparison between the dimensionless curves proposed by Katopodis and Gervais (2016) and the reviewed information for small-bodied fish species. Figure 2-1.a shows Katopodis and Gervais' dimensionless endurance curves for the complete dataset and classified by swimming mode, plotted jointly with the reviewed small-bodied fish dataset. Figure 2-1.b shows Katopodis and Gervais dimensionless endurance curves for the complete dataset and Percidae and Moronidae families, both belonging to the Perciform order, with reviewed information, collected for the same taxonomic order.



Databases from (a) Katopodis and Gervais, 2016; (b) Watson et al., 2019; (c) Laborde et al., 2016

Figure 2-1. Dimensionless endurance curves for (a) Katopodis and Gervais datasets classified by swimming mode and plotted jointly with processed endurance data for small-bodied fish species datasets; and (b) Katopodis and Gervais' datasets classified by Percidae and Moronidae families with processed endurance data for small-bodied fish species belonging to Terapontidae and Percichthydae families and Ambassis agassizzi sp., all of which belong to the Perciform order.

Similar to evidence provided in curves derived by Katopodis and Gervais (2016), the small-bodied fish species dataset shows that endurance time decreases with increased swimming velocity. Nevertheless, Katopodis and Gervais (2016) fish database and the reviewed fish database are not dimensionlessly comparable ($p > 0.01$). The small-bodied fish species dataset can be seen to the right of the general trend proposed by Katopodis and Gervais

(2016), suggesting that endurance time is higher for small-bodied fish species than for large-bodied fish in relative terms (body length). Interestingly, small-bodied endurance data for the Perciforms is not reflected in the dimensionless endurance curves for families belonging to the same order as proposed by Katopodis and Gervais (2016) ($p > 0.01$, see Figure 2-1.b).

Swimming performance based on small-bodied fish data

Small-bodied fish species with similar taxonomic characterisations to *Trichomycterus*, *Percilia* and *Diplomystes* are presented in Table 2-3, Table 2-4 and Table 2-5, respectively. Expected endurance curves for species belonging to the TDP group were estimated. Based on differences found for dimensionless endurance curves defined for small-bodied and large-bodied fish, expected TDP group endurance curves were estimated based on available information for small-bodied referenced fish species. Swimming performance of *Percilia irwini* was estimated based on *Nannoperca australis* (using reported information; Watson et al., 2019) as reference. For *N. australis* individuals with mean size of 39 mm (23 to 56 mm, total body length range, n = 25), a mean absolute critical velocity of 35 cm/s^{-1} was reported. This is equivalent to a mean relative critical velocity of 8.97 BL/s^{-1}. Consequently, for *P. irwini* with adult individuals of 55 mm (total body length range: 20 to 96 mm), expected absolute critical velocity would be around 49 cm/s^{-1} (expected critical velocity range: 18 to 86 cm/s^{-1}). Moreover, the dimensionless endurance curve proposed for *N. australis* by Watson et al. (2019) is also applicable to *P. irwini*.

Similarly, swimming performance of *Trichomycterus areolatus* was estimated based on *Trichomycterus itacarambiensis* (using reported information; Sampaio et al., 2020) as reference. Only information concerning critical velocity has been reported. For *T. itacarambiensis* individuals with mean size of 19.6 mm (total body length range: 14.5 to 23.8 mm; n = 10), a mean absolute critical velocity of 24 cm/s^{-1} was reported. This is equivalent to a mean relative critical velocity of 3.50 BL/s^{-1}. Consequently, for *T. areolatus* with adult individuals described from 55 mm (and total body length range from 25 mm to 120 mm), expected absolute critical velocity would be about 300 cm/s^{-1} (246 to 417 cm/s^{-1}; expected critical velocity range). It was not possible to estimate the swimming ability of *Diplomystes nahuelbutaensis* because similar species for which information is available are large-bodied. Based on previous results, it is known that large-bodied and small-bodied fish species are not comparable, since estimation based on large-bodied species underestimates the capabilities of small-bodied species.

Table 2-3. Taxonomically similar species to *Percilia irwini*, characterised by depth station, body length and habitat.

	Target specie	**Related species**			
Order	Perciform	Perciform	Perciform	Perciform	Perciform
Family	Percichthydae	Peciliidae	Percichthydae	Percichthydae	Percichthydae
Genus	Percilia	Nannoperca	Maccullochella	Macquaria	Macquaria
Scientific name	*Percilia irwini* 	*Nannoperca australis* 	*Maccullochella peeli* 	*Macquaria* 	*Macquaria ambigua* 
Depth station	Benthic	Benthopelagic	Benthopelagic	Benthopelagic	Benthopelagic
Body length	55 [20-96] mm (a)	Max. length SL at 10 cm. Mature males at about 30 mm and mature females at around 33 mm (c)	Max. length SL at 180 cm male/unsexed; common length 60 cm male/unsexed. Maturity at 55 cm; range 48-62 cm (e)	Max. size of about 60 cm (f)	Max. length SL at 76 cm male/unsexed; common length 45 cm male/unsexed. Maturity at 45 cm; range 40-50 cm (h)
Habitat characterisation	Rithron to potamon along rivers, mainly associated with coarse substrate (b)	Endemic to temperate rivers. Inhabits a wide variety of freshwater habitats so long as they have aquatic vegetation (d)	Oceania: throughout most of the Murray-Darling River system of South Australia, Victoria, New South Wales and Queensland, except for the upper reaches of the southern tributaries (e)	Endemic to Australia, potamotromous. Inhabits freshwater rivers, lakes and streams and moves to brackish estuaries to spawn in winter (g)	Inhabits in a range of habitat types, most commonly in slow-moving stretches of streams, lakes and backwaters. The species is restricted to freshwaters of Queensland, New South Wales, Victoria and South Australia.

(a) Valenzuela et al. (2020); (b) Garcia et al. (2012); Habit and Beck (2007); Link and Habit (2015); (c) Allen et al. (2002); (d) Paxton et al. (1989); (e) Kailola et al. (1993); Allen et al. (1989); (f) Axelrod et al. (1991); (g) Paxton et al. 1989; Allen et al. (1989); (h) Allen et al. (2002).

Table 2-4. Taxonomical similar species to *Trichomycterus areolatus*, characterised by depth station, body length and habitat.

	Target specie	**Related species**		
Order	Siluriform	Siluriform	Siluriform	Siluriform
Family	Trichomycteridae	Trichomycteridae	Trichomycteridae	Trichomcteridae
Genus	Trichomycterus	Trichomycterus	Trichomycterus	Itunglanis
Scientific name	*Trichomycterus areolatus* 	*Trichomycterus itacarambiensis* 	*Trichomycterus brasiliensis* 	*Ituglanis passensis* 
Depth station	Benthic	Benthopelagic	Benthopelagic, tropical	Benthopelagic
Body length	76 [25-120] (a)	Max. length: 8.3 cm SL (c)	Max. length: 13.5 cm SL (d)	Max. length: 7.0 cm SL (f)
Habitat characterisation	Rithral to transitional zones. Coarse substrate, slow to medium current velocity (b)	A cave-restricted species. Found mostly near the bottom and in the water column (c).	Occurs in mid-small size rivers with widths up to 8 m and transparency of about 2 m. Rivers are characterised by mainly turbulent water flow with alternating areas of currents and pools. The substrate is composed of rocks and sand (e)	Inhabits small riffles with slow current and average depth of 15-20 cm. Exhibits crypto-biotic habits, hiding in the gravel bottom or under limestone blocks (f)

(a) Manriquez et al., 1988 (b) Arratia, 1983; Penaluna et al. 2009; Scott et al. 2007; (c) Trajano et al. 1997; (d) Triques and Vono, 2004; (e) Lima et al. 2013; Fernandez and Bichuette, 2002.

Table 2-5. Taxonomically similar species to *Percilia irwini*, characterised by depth station, body length and habitat.

	Target specie	**Related species**	
Order	Siluriform	Siluriform	Siluriform
Family	Diplomystidae	Ictaluridae	Ictaluridae
Genus	Diplomystes	Ictalarus	Ictalarus
Scientific name	*Diplomystes nahuelbutaensis* 	*Ictalarus punctatus* 	*Ictalarus furcatus* 
Depth station	Benthic	Benthic, subtropical	Benthic, subtropical
Body length	57 [25-115] (a)	Maturity: Lm 43.1, range 54-67.2 cm. Max length: 132 cm TL (c)	Max. length: 165 cm TL (e)
Habitat characterisation	Rithral zones with coarse substrate; zones with high turbulence and dissolved oxygen and low temperature (b)	Inhabits lakes and deep pools and runs over sand or rocks in small to large rivers. Adults occur in rivers and streams and prefer clean, well oxygenated water, but are also found in ponds and reservoirs (d)	Inhabits deep water in impoundments and main channels and backwaters of medium to large rivers, over mud, sand and gravel. Stays on the bottom during the day in deep areas and moves into swifter water at night to feed. Prefers clear, strongly flowing water

(a) Vila et al., 1996; Beltrán-Concha et al., 2012 (b) Arratia, 1983, 1987; Penaluna, 2009; (c) Page and Burr 2011; (d) Frimodt, 1995; Yamamoto and Tagawa, 2000; (e) Page and Burr 1991; (f) Page and Burr 2011; NatureServe, 2013.

Expected swimming distance

Curves produced by Peake et al. (1997) were used to estimate allowable fishway lengths. For *Percilia irwini*, maximum allowable flow velocity for fishways with lengths ranging from 2 to 100 m equate to 66.9 cm/s^{-1} [up to 86.7 cm/s^{-1}] to 40.9 cm/s^{-1} [up to 41.2 cm/s^{-1}] (Figure 2).

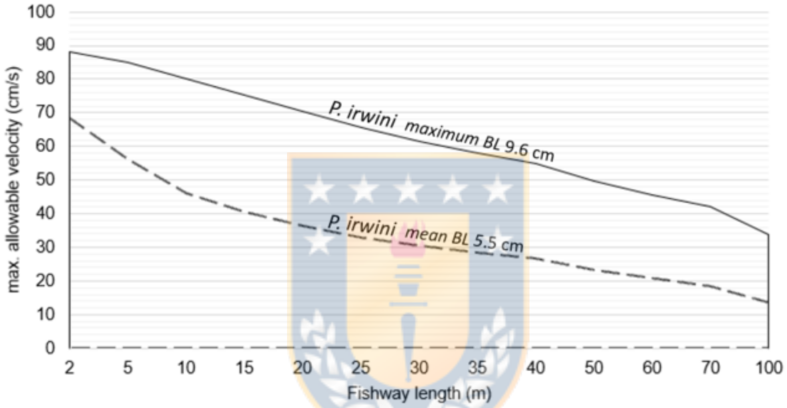


Figure 2-2. Maximum allowable flow velocity over fishway length for *Percilia irwini*, based on estimated endurance (according to Watson et al., 2019).

Turbulence and kinematics

Another factor affecting fish swimming performance is the scale and intensity of turbulence in the flow (Nikora et al., 2003). Available information on small-bodied fish kinematics is limited. Knapp et al. (2019) presented an overview of studies capturing the flow field for the purpose of correlation with fish swimming performance to evaluate fish passage. Link et al. (2017) found that two native

Chilean fish species exhibit notably different swimming styles when confronted with a von Kármán vortex street. While *Basilichthys microlepidotus* sp. managed to partially adapt its swimming gait to the ensuing regular vortex street, thus maintaining stability, *Cheirodon galusdae* was repeatedly destabilised by the turbulence. Adaptation to regular von Kármán turbulence in order to conserve or regenerate energy is known as the Kármán gait (Liao, 2007; Liao and Cotel, 2013). Fish also use other approaches for saving or regenerating energy, such as bow waking upstream of an obstacle or entraining on either side of one (Trinci et al., 2017). These methods all suggest that fish can anticipate the flow and thus require either a static or regularly periodic flow field. On the other hand, turbulence that is unpredictable for fish can more easily destabilise them. The negative influence of turbulence on fish has, for example, been discussed by Lupandin (2005), who observed the effects of flow turbulence on the swimming capabilities of perch (*Perca fluviatilis*). The study indicates that the body length of the fish and critical turbulence length scale are correlated. Smaller eddies acting on the body of the fish can, for the most part, balance each other out when the fish travels through them. Larger eddies at or above the critical turbulence length scale may exert a torque on the fish for which there is no counteracting eddy and which consequently creates an imbalance. Magaju et al. (2020) present an overview of studies performed to understand fish behaviour in a turbulent flow condition using different flow generators. Kinematics, including tail beat frequency (TBF), tail beat amplitude (TBA), shape of fish body and mode of locomotion (Webb, 1988; Blake,

2004) are important for designing effective fishways. In general, TBF is inversely related to body mass and directly related to fish swimming velocity (Videler and Wardle, 1991). Researchers have reported a linear relationship between TBF and velocity (Parsons et al., 2003; Cai et al., 2013). The TBA is also a function of fish swimming velocity, and linear and exponential increments have been reported (Cai et al., 2013). Interestingly, this difference is due to different swimming modes (Katopodis et al., 2019).

International Fish Passage Development for Small-Bodied Species

As the goal of conservation activities shifts from a maximum-sustainable-yield to a biodiversity-protection approach, it will be increasingly important to consider the swimming abilities and behaviour of the complete fish community (Oldani et al., 2007). The New Zealand Fish Passage Guidelines (2018) set the main objectives for suitable design of instream structures and gives recommendations for culverts and weirs.

Fishway type is one of the most important decisions when considering fishway design. Passage of small-bodied fish species can be facilitated by adding baffles (Newbold et al., 2014; David et al., 2014), and a decrease in baffle spacing can improve passage of small-bodied fish (Cabonce et al., 2019; Jones et al., 2020). In this sense, fishways that provide diverse flow conditions are likely to be most successful in allowing passage of groups of fish with contrasting swimming abilities (Bunt et al., 2012; Williams et al., 2012). Research indicates that passage success is influenced by factors such as ramp length, slope and substrate, but that it also varies between species and fish sizes (Baker, 2014; Doehring et al., 2012). Likewise, weir-style baffles have been suggested as a suitable mitigation option for small-bodied fish (Ead et al., 2002), with fish making better upstream progress when a pathway along the culvert base is provided (e.g., through spoiler baffles; Feurich et al., 2012).

Target species has a significant effect on passage performance. Fish length is a biological factor with clear influence on swimming performance (Beamish, 1978; Haro et al., 2004; Ruiz-Legazpi et al., 2018). Jones et al. (2020) indicate that more benthic-swimming species were able to maintain position in low flow velocities with relative ease by holding position using pectoral fins, while the more pelagic species had to expend substantially more energy by active swimming. Moreover, *Trichomycterus* and *Diplomystes* (both benthic species) have a smooth abdomen, enabling them to resist high water velocities and rest by temporarily skimming the bottom. Impact of substrate type (smooth or rough) for other species with the same body shape has been studied. Available information showed no clear preference for a specific substrate (Downie and Kieffer, 2017). This swimming behaviour would provide rest while moving through a fishway. To effectively mitigate barrier impacts, fishway design should aim to provide passage for all individuals (Baras and Lucas, 2001).

Slope has been shown to have a significant relationship with both passage success (negative effect, i.e., the greater the slope, the lower the success) and transit time (positive effect, i.e., the greater the slope, the lower the transit time; Noonan et al., 2012; Bunt et al., 2012). Quaranta et al. (2019) found a similar relationship between passage success relating to lower slopes and more compatible hydraulic conditions for fish swimming capabilities. According to the New Zealand Fish Passage Guidelines, the slope should be gentle (1:15 to 1:30). A slope of 1:30 is suitable where weakly swimming species such as inanga and smelt require passage. The passage slope should be minimised and, as a general rule of thumb, be less than 1:10 for fall heights of ≤ 1 m and less than 1:15 for fall heights of 1-4 m. The fishway should create a hydraulically diverse flow environment including low-velocity margins and resting areas. Roughness elements should be added to the weir face. A continuous low-velocity wetted margin should be provided up the weir throughout the fishway design flow range.

Total fishway height is key to fish passage. It arises from the hypothesis that fish show differences depending on the accumulated height ascended, for example, due to fatigue. Transit time shows a direct relationship between fatigue and height (i.e., the higher the barrier, the slower the ascent; Bunt et al., 2012). Fish fatigue must be considered in fishway design. Fish need to rest when fatigued before continuing through a fishway, and incomplete recovery decreases swimming capability (Jain and Farrell, 2003; Cai et al., 2014). Energy expenditure may be more closely related to fishway steepness than length; fishway length and slope were found to be negatively correlated (Mallen-Cooper and Stuart, 2007).

Design criteria applied for TDP group passage

According to the swimming capacities and behaviour expected for the TDP group and the revised fishway design recommendations, especially considering those aimed at small-bodied species, suitable design conditions are projected for the passage of this priority assemblage. A baffle design with flow rates up to 41.2 cm/s^{-1}, water depth of at least 2.5 cm, and maximum slope of 1:15 is expected to be suitable for the TDP group. According to the total height of the obstacle, maximum continuous fishway length should be evaluated and rest pools incorporated as necessary.

Discussion

While swimming performance is an important consideration for fishway design, obtaining detailed data on every species and size class is not always logistically feasible. Especially complex is the situation with small-bodied species, because they are not of commercial interest and inhabit regions with large rivers, making their capture and/or field testing difficult. Fortunately, there is growing interest worldwide in non-salmonid species, and for groups of different species simultaneously. However, anthropogenic pressures for development in some regions reduce the time needed to fill these gaps in knowledge. Dimensionless generalisations and correlations with fish species characteristics found in the literature have been proposed to estimate the swimming capacities of species, providing information that was previously unavailable. Consequently, the present study aimed to estimate swimming performance for a small-bodied target group – the TDP group – as a study case identified as a priority for fishway development in Chile. Swimming capacities were estimated based on a literature review. First, the available information on swimming abilities for the genera present in the TDP group was reviewed, covering both large-bodied and small-bodied fish species. Then, the applicability of the generalised curves proposed by Katopodis and Gervais (2016) for small-bodied species was analysed. Species with similar characteristics to the species present in the TDP group were then reviewed. This enabled estimation of endurance curves for the TDP group. Finally, based on expected swimming performance for TDP group fish species and their body length range, expected distance design curves as proposed by Peake (1997) were calculated.

We selected the TDP group as a small-bodied fish assemblage study case. This group of Chilean species is identified as a priority for development of mitigation technology in response to the extensive hydroelectric development expected for the region in which they are found. Our main results suggest that, despite the lack of extensive small-bodied swimming performance data for small-bodied fish species, the information available is sufficient for the estimation of a comprehensive criterion of capabilities and behaviour. Nevertheless, swimming performance for small-bodied fish species should be estimated based on information available for other similar small-bodied fish species.

Differences were observed in the dimensionless swimming capacity of small-bodied versus large-bodied fish species in the same taxonomic order, suggesting scale effects. Small-bodied species are more capable in relative terms (BL/s^{-1}), than large-bodied species. In general, large-bodied species have been described as not exceeding the threshold of 10 BL/s; however, the reviewed literature presents results that exceed 15 BL/s for small-bodied species. Similar results were reported by Laborde et al. (2016) for *Cheirodon galusdae* and *Basilichthys microlepidotus*, two Chilean native species. The last could be explained by small-bodied energy saving strategies and/or physiological differences. First, small-bodied fish species may employ energy-saving strategies, utilising boundary layers to reduce the velocity challenges found within structures (Goodrich et al., 2018; Watson et al., 2018). Second, while some studies have reported linear relationships between fish swimming velocity and body length (Hammer, 1995; Hou et al., 2018), the underlying relationships are allometric rather than isometric. The physiology of most animals, including fish, is allometric (Cai et al., 2020). Drag force scales in proportion to the surface area of a fish, increasing in proportion to the square of the body length, while the muscle powering locomotion scales with volume and increases in proportion to the cube of the body length. The specific relationship between muscle weight and drag force is complex and changes with fish shape and size. As fish size increases, the relative values of surface area and muscle weight scale such that absolute swimming velocity increases while relative swimming velocity decreases. Finally, according to the information available for small-bodied species of the same taxonomic order, it was possible to estimate the swimming capacity of *P. irwini*.

Current approaches used to estimate swimming performance have limitations, including the selection of representative flow velocities for fish swimming time-to-fatigue. Specifically, the commonly employed average cross-sectional velocity is not representative of the hydrodynamics experienced by some fish, since fish swim close to the channel bed where the flow velocity is lower. The dimensions of the channel used to test fish swimming performance can have an important influence on swimming performance curves. Kerr et al. (2020) showed that burst-and-coast swimming was increasingly observed for near-bottom velocities exceeding 0.2 m/s^{-1} (i.e., average cross-sectional velocity

> 0.3 m/s^{-1}). This suggests that the burst-and-coast swimming mode is beneficial under higher velocities because intermittent swimming bestows energetic benefits. Indeed, it is well known that gait transitions, including burst-and-coast swimming, enable recovery and thus enhanced swimming performance (Tudorache et al., 2008; Peake et al., 1997). Failure to provide sufficient test space can prevent the subject fish from displaying behaviours that can enhance performance, resulting in conservative estimates of swimming capability (Tudorache et al., 2008). The average cross-sectional velocity is clearly not representative of the swimming conditions of bottom-dwelling fish like *Trichomycterus* and *Diplomystes*, which gain energetic advantages by exploiting the low velocities that characterise near-wall flow regions.

It is important to note certain limitations regarding the use of available datasets, categorisation of the information, and assumptions that can be made. First, not all taxonomic orders are found in different regions of the world, and furthermore, not all taxonomic orders include small- and large-bodied representatives with which to make comparisons. Although body length is one of the relevant characteristics, there are many factors that affect swimming ability (e.g., temperature, sex and maturity). Second, the available information has not been obtained in the same way, with variations in the individuals tested: wild versus captive (Basaran et al., 2007), different sampling sizes and different body ranges. Most research considers the effect of a single factor such as temperature, water velocity or dissolved oxygen on swimming performance. Thus, studies do not precisely reflect the physical relationship between factors. Greater evaluation of multiple factors and the interactions between those factors is needed in order to improve multivariate models of swimming performance and more accurately reflect representative conditions. The effect of temperature on fish passage has received less attention and its contribution to the ability of native fish to negotiate obstacles remains speculative (Boubeé et al., 1999). However, temperature effects might be an important topic in the study region given highly dynamic diel fluctuations observed in water temperature. Link et al. (2013) reported fluctuations of up to 10°C in river temperatures in summer in central Chile. There are also differences between the tests performed (swimming chamber versus channel, different time intervals, etc.). While unconstrained, fish could exhibit burst-and-coast swimming and exploit low-velocity areas available within the flume to conserve energy. Compared to that observed in the swim chamber trials, performance may have been expected to be higher as a consequence (Peake and Farrell, 2004). Future studies should include investigation of methodological issues, comparison of metrics between methods, calibration of results from laboratory and field swimming performance tests and, where feasible, analysis of the efficacy of swim test data on the design of successful fishways. Moreover, the use of volitional swim tests conducted in real or simulated open channels may impact results, because many species, including *Percilia*, T*richomycterus* and other galaxiids and darter species, employ specialised swimming or movement techniques, such as the use of pectoral fins to climb or hold station (Carlson and

Lauder, 2011; Peake et al., 1997). For example, Watson et al. (2019) reported that, during trials, *H. compressa*, *H. galii*, *M. adspersa*, *P. grandiceps and R. bikolanus* all displayed station holding behaviour, particularly when swimming at velocities that were not challenging. At challenging velocities, these species were unable to utilise station holding due to losing their grip on the smooth surfaces in the experimental equipment. Plew et al. (2007) studied the burst-and-coast swimming of *G. maculatus* by videoing fish trajectories. Similar results were obtained by Gischke (2016) in experiments with *Trichomycterus*: the swimming chamber limited its capacity because it adopted a burst-and-coast swimming mode. Fishway structures generally have a rough surface, making it reasonable to anticipate that climbing and station holding species may be capable of withstanding faster water velocities in a real situation than what was observed in the experimental flumes (as suggested by Tudorache et al., 2008 and Castro-Santos et al., 2013). Furthermore, a fish's motivation to perform is hard to quantify in both the field and the laboratory (Goerig et al., 2019).

Laboratory-defined fish swimming performance data has been used extensively in the design of fishway structures in many parts of the world (Link et al., 2017; Botha et al., 2018; Cai et al., 2018; Katopodis et al., 2019). According to several researchers (Cada and Odeh, 2001; Nikora et al., 2003; Cotel et al., 2006), the turbulence properties of a fishway might correlate with fish behaviour. Turbulence is indicative of velocity dispersion in the flow field and can be represented with several quantities. Interestingly, Lupandin (2005) observed that vortices have a strong effect on fish locomotion when the dimensionless length-scale is higher than 2/3 fish length. Link et al. (2017) found that two native Chilean fish species exhibited distinctly different swimming styles when confronted with a von Kármán vortex street. While *B. microlepidotus* species managed to partially adapt its swimming gait to the ensuing regular vortex street, thus maintaining stability, *Ch. galusdae* was repeatedly destabilised by the turbulence. *Percilia* is expected to adopt a station holding strategy, and *Trichomycterus* and *Diplomystes* to a burst-and-coast swimming mode under non-motivating flow conditions.

Finally, to validate the passage design proposal for the TDP group, passage effectiveness of baffle configurations should be tested due to the widely discussed intraspecific and interspecific variation in fish swimming performance. Furthermore, in order to continue advancing in the development of mitigation technologies to minimise the impacts of instream structures on small-bodied fish species, further research on small-bodied fish behaviour and its response to complex fishway hydraulics is necessary.

Conclusion

This study aimed to estimate swimming performance for a small-bodied target group – the TDP group – as a study case identified as a priority for fishway development in Chile. Swimming capacities were estimated based information obtained from the literature concerning the applicability of proposed dimensionless variables and a proposed correlation of swimming capacities with fish species characteristics. Three key results are identified. (1) Dimensionless swimming capacities of small-bodied and large-bodied fish species are not comparable, even for the same taxonomic order, suggesting scale effects. (2) Based on the taxonomic characterisation, depth station, body size and habitat of the species belonging to the TDP group, species with similar characteristics were identified and their proposed dimensionless endurance were applied to *Trichomycterus*, *Percilia* and *Diplomystes*. (3) Based on estimated swimming performance and body length range for *P. irwini*, distance design curves as proposed by Peake (1997) were calculated. Finally, the relevance and limitations of small-bodied swimming performance data in fishway design are discussed and a baffle design is proposed as a suitable design for the TDP group.

Further research on small-bodied fish motion and hydraulics, focused on how flow influences fish behaviour and vice versa (i.e., ethohydraulics), is needed in order to develop suitable fishway designs for small-bodied fish species.

Acknowledgements

The financial support provided by the Chilean Agency for Innovation and Development (ANID) though grant 21160737: “Development of fishways for longitudinal connectivity of Chilean rivers threatened by small hydropower plants”, and FONDECYT 1150154: ‘Within watershed barriers and among-watershed leaks: changing connectivity of rivers in central Chile and its impact on native fish” is gratefully acknowledged.

References

Allen, P.J., Hodge, B., Werner, B., Cech, J.J., 2006. Effects of ontogeny, season, and temperature on the swimming performance of juvenile green sturgeon (Acipenser medirostris). Can. J. Fish. Aquat. Sci. 63, 1360–1369.

Arratia F, G. 1983. Preferencias de habitat de peces siluriformes de aguas continentales de Chile (Fam. Diplomystidae y Trichomycteridae). *Studies on Neotropical Fauna and Environment*, *18*(4), 217-237.

Baker C. 2014. Effect of ramp length and slope on the efficacy of a baffled fish pass. J Fish Biol. 84(2): 491–502.

Baras E, Lucas M. 2001. Impacts ofman's modifications of river hydrology on the migration of freshwater fishes: a mechanistic perspective. Ecohydrol Hydrobiol 1: 291–304.

Basaran, F., Ozbilgin, H., Ozbilgin, Y., 2007. Comparison of the swimming performance of farmed and wild gilthead sea bream, Sparus aurata. Aquac Res 38, 452–456.

Beamish, F. 1966. Swimming endurance of some Northwest Atlantic fishes. *Journal of the Fisheries Board of Canada*, *23*(3), 341-347.

Beamish FW. 1978. Swimming capacity: 101–187. In Fish Physiology 7: Locomotion, Hoar WS, Randall DJ (eds). Academic Press: London.

Beecham, R. V., Pearson, P. R., LaBarre, S. B., & Minchew, C. D. (2009). Swimming performance and metabolism of cultured golden shiners. *North American Journal of Aquaculture*, *71*(1), 59-63.

Beltrán-Concha, M., Muñoz-Ramírez, C., Ibarra, J., & Habit, E. (2012). Análisis de la dieta de Diplomystes (Siluriformes: Diplomystidae) de Chile. *Gayana (Concepción)*, *76*(2), 102-111.

Birnie-Gauvin, K., Candee, M. M., Baktoft, H., Larsen, M. H., Koed, A., & Aarestrup, K. (2018). River connectivity reestablished: E ffects and implications of six weir removals on brown trout smolt migration. River Research and Applications, 34(6), 548-554.

Blake, R.W., 2004. Fish functional design and swimming performance. J. Fish Biol. 65, 1193–1222.

Botha, T., Mahloko, M., Wepener, V., Howatson, G., Smit, N., 2018. A tool for determining maximum sustained swimming ability of selected inland fish species in an Afrotropic ecozone. Water Sa 44, 511 5.

Boubée JA, Jowett IG, Nichols S, Williams EK. 1999. Fish Passage at Culverts: A Review with Possible Solutions for New Zealand Indigenous Species. Department of Conservation, Wellington, New Zealand. Available at http://www.doc.govt.nz/Documents/scienceand-technical/ culverts01.pdf/

Braaten, P.J., Elliott, C.M., Rhoten, J.C., Fuller, D.B., McElroy, B.J., 2015. Migrations and swimming capabilities of endangered pallid sturgeon (Scaphirhynchus albus) to guide passage designs in the fragmented Yellowstone River. Restor. Ecol. 23, 186–195.

Brett, J. 1964. The respiratory metabolism and swimming performance of young Sockeye salmon. J. Fish. Board Can. 21, 1183–1226

Brett, J. 1967. Swimming performance of sockeye salmon (Oncorhynchus nerka) in relation to fatigue time and temperature. Journal of the Fisheries Board of Canada, 24(8), 1731-1741.

Bunt C, Castro-Santos T, Haro A 2012. Performance of fish passage structures at upstream barriers to migration. River Res Appl 28: 457–478.

Burgess, E., Booth, D., & Lanyon, J. 2006. Swimming performance of hatchling green turtles is affected by incubation temperature. *Coral reefs*, *25*(3), 341-349.

Cabonce J, Fernando R, Wang H, Chanson H (2019) Using small triangular baffles to facilitate upstream fish passage in standard box culverts. Environ Fluid Mech 19: 157–179.

Cada, G. F., & Odeh, M. (2001). Turbulence at Hydroelectric Power Plants and its Potential Effects on Fish (No. DOE/BP-26531-1). Bonneville Power Administration, Portland, OR (US).

Cai, L., Chen, J., Johnson, D., Tu, Z., & Huang, Y. (2020). Effect of body length on swimming capability and vertical slot fishway design. Global Ecology and Conservation, 22.

Cai, L., Katopodis, C., Johnson, D., Zhang, P., Zhao, P., 2018. Case study: targeting species and applying swimming performance data to fish lift design for the Huangdeng Dam on the upper Mekong River. Ecol. Eng. 122, 32e38.

Cai, L., Liu, G., Taupier, R., Fang, M., Johnson, D., Tu, Z., Huang, Y., 2014. Effect of temperature on swimming performance of juvenile Schizothorax prenanti. Fish Physiol. Biochem. 40, 491e498.

Cai, L., Taupier, R., Johnson, D., Tu, Z., Liu, L., Huang, Y., 2013. Swimming capability and swimming behavior of juvenile Acipenser schrenckii. J. Exp. Zool. Part A 319, 149–155.

Carlson, R., Lauder, G. 2011. Escaping the flow: boundary layer use by the darter Etheostoma tetrazonum (Percidae) during benthic station holding. Journal of Experimental Biology, 214(7), 1181-1193.

Castro-Santos, T., Sanz-Ronda, F., Ruiz-Legazpi, J. 2013. Breaking the velocity limit—comparative sprinting performance of brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta). Can. J. Fish. Aquat. Sci. 70, 280-293.

Cocherell, D.E., Kawabata, A., Kratville, D.W., Cocherell, S.A., Kaufman, R.C., Anderson, E.K., Chen, Z.Q., Bandeh, H., Rotondo, M.M., Padilla, R., Churchwell, R., Kavvas, M., CechJr, J., 2011. Passage performance and physiological stress response of adult White sturgeon ascending a laboratory fishway. J. Appl. Ichthyol. 27, 327–334.

Cano-Barbacil, C., Radinger, J., & García-Berthou, E. (2020). Reliability analysis of fish traits reveals discrepancies among databases. *Freshwater Biology*, *65*(5), 863-877.

Cotel AJ, Webb PW, Tritico H (2006) Do brown trout choose locations with reduced turbulence? Trans Am Fish Soc 135:610–619.

Cussac, V. E., Fernández, D. A., Gómez, S. E., & López, H. L. 2009. Fishes of southern South America: a story driven by temperature. Fish Physiology and Biochemistry, 35(1), 29-42.

Díaz, G., Arriagada, P., Górski, K., Link, O., Karelovic, B., Gonzalez, J., & Habit, E. (2019). Fragmentation of Chilean Andean rivers: expected effects of hydropower development. Revista chilena de historia natural, 92(1), 1-13.

Doehring, K., Young, R., McIntosh, A. 2012. Facilitation of upstream passage for juveniles of a weakly swimming migratory galaxiid. New Zealand Journal of Marine and Freshwater Research, 46(3), 303-313.

Downie, A., Kieffer, J. 2017. Swimming performance in juvenile shortnose sturgeon (Acipenser brevirostrum): the influence of time interval and velocity increments on critical swimming tests. Conservation physiology, 5(1).

Duan, M., Qu, Y., Zhuang, P., 2018. Swimming characteristics of the siberian sturgeon. Book: the Siberian Sturgeon (Acipenser Baerii, Brandt, 1869) Volume 1 - Biology. Springer, Cham., pp. 229–246.

Dupont, D. 2020. Quantifying Swimming Performances of Freshwater Fishes Native to New Zealand Using Ucrit and Usprint Tests.

Dyer B. 2000. Systematic review and biogeography of the freshwater fishes of Chile. Estudios Oceanológicos 19: 77–98.

Ead, S. A., Rajaratnam, N., & Katopodis, C. 2002. Generalized study of hydraulics of culvert fishways. Journal of Hydraulic Engineering, 128(11), 1018-1022.

Feurich, R., Boubée, J., & Olsen, N. R. B. (2012). Improvement of fish passage in culverts using CFD. Ecological Engineering, 47, 1-8.

Franklin, P. A., Gee, E., Baker, C. F., & Bowie, S. (2018). New Zealand fish passage guidelines. Hamilton: National Institute of Water and Atmospheric Research.

Franklin, P., & Gee, E. (2019). Living in an amphidromous world: Perspectives on the management of fish passage from an island nation. Aquatic Conservation: Marine and Freshwater Ecosystems, 29(9), 1424-1437.

García A, Sobenes C, Link O, Habit E. 2012. Bioenergetic models of the threatened darter Percilia irwini. Marine and Freshwater Behavior and Physiology 45: 17–28.

Geist, D.R., Brown, R.S., Cullinan, V., Brink, S.R., Lepla, K., Bates, P., Chandler, J.A., 2005. Movement, swimming velocity, and oxygen consumption of juvenile White sturgeon in response to changing flow, water temperature, and light level in the Snake River, Idaho. T. Am. Fish. Soc. 134, 803–816

Gischke A. 2014. Design criteria in fish passes for the Chilean catfish Trichomycterus areolatus. Master Thesis. Magdeburg University of Applied Sciences pp: 62.

Goerig, E., Castro-Santos, T. 2017. Is motivation important to brook trout passage through culverts?. Canadian Journal of Fisheries and Aquatic Sciences, 74(6), 885-893.

Habit, E., Dyer, B., Vila, I. 2006. Estado de conocimiento de los peces dulceacuícolas de Chile. Gayana 70(1): 100–113

Habit, E., García, A., Díaz, G., Arriagada, P., Link, O., Parra, O., Thoms, M. 2018. River science and management issues in Chile: hydropower development and native fish communities. River Res Appl. (special issue paper):1- 11.

Habit, E., Dyer, B., Vila, I. 2006. State of knowledge of freshwater fish in Chile. Gayana (Concepción) , 70 (1), 100-113.

Haefner, J., Bowen, M., 2001. Physical-based model of fish movement in fish extraction facilities. Ecol. Model. 152, 227–245.

Hammer C. 1995. Fatigue and exercise tests with fish. Comparative Biochemistry and Physiology 112A: 1–20.

Haro, A., Castro-Santos, T., Noreika, J., Odeh, M. 2004. Swimming performance of upstream migrant fishes in open-channel flow: a new approach to predicting passage through velocity barriers. Can J Fish Aquat Sci 61: 1590–1601.

Hoover, J.J., Adams, S.R., Killgore, K.J., 2003. Can Hydraulic Barriers Stop the Spreadof the Round Goby? TN ANSRP-03-1, U.S. Army Corps of Engineers, US ArmyEngineer Research and Development Center (ERDC). Vicksburg, MS.

Hou, Y., Cai, L., Wang, X., Chen, X., Zhu, D., Johnson, D., Shi, X., 2018. Swimming performance of twelve Schizothoracinae species from five rivers. J. Fish. Biol. 92, 2022–2028.
Jager, H., Parsley, M., Cech, J., McLaughlin, R., Forsythe, P., Elliott, R., Prachell, B. 2016. Reconnecting fragmented sturgeon populations in North American rivers. Fisheries 41, 141–148.

Jain, K., Farrell, A. 2003. Influence of seasonal temperature on the repeat swimming performance of rainbow trout Oncorhynchus mykiss. Journal of Experimental Biology, 206(20), 3569-3579.

Jones, P., Svendsen, J., Börger, L., Champneys, T., Consuegra, S., Jones, J., Garcia de Leaniz, C. 2020. One size does not fit all: inter-and intraspecific variation in the swimming performance of contrasting freshwater fish. Conservation physiology, 8(1), coaa126.

Katopodis C. 1992. Introduction to Fishway Design. Freshwater Institute, Central and Arctic Region, Department of Fisheries and Oceans: Winnipeg, Manitoba, Canada.

Katopodis C. 1994. Analysis of ichthyomechanical data for fish passage or exclusion system design. In High-Performance Fish: Proceedings of an

International Fish Physiology Symposium, MacKinlay DD (ed). American Fisheries Society, Physiology Section, Bethesda: Maryland; 318–323.

Katopodis, C. 2005. Developing a toolkit for fish passage, ecological flow management and fish habitat works. Journal of Hydraulic Research, 43(5), 451-467.
Katopodis, C., Cai, L., Johnson, D. 2019. Sturgeon survival: The role of swimming performance and fish passage research. Fisheries Research, 212, 162-171.

Katopodis, C., Gervais, R., 2016. Fish Swimming Performance Database and Analyses. DFO Canadian Science Advisory Secretariat Research Document 2016/002. vi +. pp. 550.

Katopodis, C., Williams, J., 2016. Not all fishways are created equal. Paper 26152. In: Webb, J.A., Costelloe, J.F., Casas-Mulet, R., Lyon, J.P., Stewardson, M.J. (Eds.), Proceedings of the 11th International Symposium on Ecohydraulics. University of Melbourne, Melbourne, Australia 7-12 February 2016.

Kern, P., Cramp, R., Gordos, M., Watson, J., Franklin, C. 2018. Measuring U crit and endurance: equipment choice influences estimates of fish swimming performance. *Journal of fish biology*, *92*(1), 237-247.

Killen, S. S., Glazier, D. S., Rezende, E. L., Clark, T. D., Atkinson, D., Willener, A. S., & Halsey, L. G. (2016). Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. *The American Naturalist*, *187*(5), 592-606.

Kolok, A. S. (1999). Interindividual variation in the prolonged locomotor performance of ectothermic vertebrates: a comparison of fish and herpetofaunal methodologies and a brief review of the recent fish literature. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*(4), 700-710.

Knapp, M., Montgomery, J., Whittaker, C., Franklin, P., Baker, C., Friedrich, H. 2019. Fish passage hydrodynamics: insights into overcoming migration challenges for small-bodied fish. Journal of Ecohydraulics, 4(1), 43-55.

Laborde, A., González, A., Sanhueza, C., Arriagada, P., Wilkes, M., Habit, E., Link, O. 2016. Hydropower development, riverine connectivity, and non-sport fish species: Criteria for hydraulic design of fishways. River Research and Applications, 32(9), 1949-1957.

Laborde, A., Habit, E., Link, O., Kemp, P. 2020. Strategic methodology to set priorities for sustainable hydropower development in a biodiversity hotspot. Science of The Total Environment, 714, 136735.

Lacey RW, Neary VS, Liao JC, Enders EC, Tritico HM. 2012. The IPOS framework: linking fish swimming performance in altered flows from laboratory experiments to rivers. River Research and Applications 28: 429–443.

Liao, J., Beal, D., Lauder, G., Triantafyllou, M. 2003. The Kármán gait: novel body kinematics of rainbow trout swimming in a vortex street. Journal of experimental biology, 206(6), 1059-1073.

Liao J., Beal D., Lauder G., Triantafyllou M. 2003b. Fish exploiting vortices decrease muscle activity. Science 302:1566–1569.

Liao J., Cotel A. 2013. Effects of turbulence on fish swimming in aquaculture. In: Palstra AP, Planas JV, editors. Swimming Physiology of Fish - Towards Using Exercise to Farm a Fit Fish in Sustainable Aquaculture. Berlin, Heidelberg: Springer-Verlag. Chapter 5; p. 109–128.
Liao, J. 2007. A review of fish swimming mechanics and behaviour in altered flows. Philosophical Transactions of the Royal Society B: Biological Sciences, 362(1487), 1973-1993.

Link O, Habit E. 2015. Requirements and boundary conditions for fish passes of non-sport fish species based on Chilean experiences. Reviews in Environmental Sciences and Biotechnology 14(1): 9–21.

Link O, Huerta A, Stehr A, Monsalve A, Meier C, Aguayo M. 2013. The solar to stream power ratio: a dimensionless number explaining diel fluctuations of temperature in mesoscale rivers. River Res Appl 29(6):792–803

Link O, Sanhueza C, Arriagada P, Brevis W, Laborde A, Gonzalez A, Wilkes M, Habit E. 2017. The fish Strouhal number as a criterion for hydraulic fishway design. Ecol Eng. 103(Part A):118–126. Lintermans M. 2016. Conservation status

Long, J. 1995. Morphology, mechanics, and locomotion: the relation between the notochord and swimming motions in sturgeon. Environ. Biol. Fish. 44, 199–211.

Lupandin, A. 2005. Effect of flow turbulence on swimming velocity of fish. Biol Bull. 32(5):461–466.

Magaju, D., Montgomery, J., Franklin, P., Baker, C., Friedrich, H. 2020. A new framework for assessing roughness elements in promoting fish passage at low-head instream structures. Journal of Ecohydraulics, 5(2), 152-164.

Mallen-Cooper, M., Stuart, I. 2007. Optimising Denil fishways for passage of small and large fishes. Fisheries Management and Ecology, 14(1), 61-71.

Manriquez, A., Huaqúin, L., Arellano, M., & Arratia, G. (1988). Aspectos reproductivos de Trichomycterus areolatus Valenciennes, 1846 (Pisces: Teleostei: Siluriformes) en río Angostura, Chile. *Studies on Neotropical Fauna and Environment*, *23*(2), 89-102.

McKenzie, D.J., Cataldi, E., Romano, P., Owen, S.F., Taylor, E.W., Bronzi, P., 2001. Effects of acclimation to brackish water on the growth, respiratory metabolism, and swimming performance of young-of-the-year Adriatic sturgeon (Acipenser naccarii). Can. J. Fish. Aquat. Sci. 58, 1104–1112.

Monsalve, A., Link, O., Stehr, A. 2012. Régimen Térmico de Ríos: Desarrollo, Verificación y Aplicación de un Modelo Numérico. Tecnología y Ciencias del Agua 3(4):41–56

Muraoka, K.; Nakanishi, S.; Kayaba, Y. Boulder arrangement on a rocky ramp fishway based on the swimming behavior of fish. Limnologica 2017, 62, 188–193. Myers N, Mittermeier R,Mittermeier C, Da Fonseca G, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403(6772): 853–858.

Newbold L., Karageorgopoulos P, Kemp P. 2014. Corner and sloped culvert baffles improve the upstream passage of adult European eels (Anguilla anguilla). Ecol Eng 73: 752–759.

Nikora V, Aberle J, Biggs BJ, Jowett I, Sykes JR. 2003. Effects of fish size, time-to-fatigue and turbulence on swimming performance: a case of study of Galaxias maculatus. Journal of Fish Biology 63: 1365–1382.

Noonan, M.J., Grant, J.W.A., Jackson, C.D., 2012. A quantitative assessment of fish passage efficiency. Fish Fish. 13, 450–464.

Oldani, N.O., Baigun, C.R.M., Nestler, J.M. and Goodwin, R.A. (2007) Is fish passage technology saving fish resources in the lower La Plata River basin? Neotropical Ichthyology 5, 89–102.

Parsons, G.R., Hoover, J.J., Killgore, K.J., 2003. Effect of Pectoral fin ray removal stationholding ability of shovelnose sturgeon. N. Am. J. Fish. Manag. 23, 742–747.

Pavlov, D. S. (1989). Structures assisting the migrations of non-salmonid fish: USSR (Vol. 308). Food & Agriculture Org.

Peake S., Beamish F., McKinley R., Scruton D., Katopodis C. 1997. Relating swimming performance of lake sturgeon, Acipenser fulvescens, to fishway desing. Canadian Journal of Fisheries and Aquatic Sciences 54(6): 1361–1366.

Peake, S., Farrell, A. 2004. Locomotory behaviour and post-exercise physiology in relation to swimming velocity, gait transition and metabolism in free-swimming smallmouth bass (Micropterus dolomieu). Journal of Experimental Biology, 207(9), 1563-1575.

Peake, S. J. (2008). Gait transition speed as an alternate measure of maximum aerobic capacity in fishes. *Journal of fish biology*, *72*(3), 645-655.

Penaluna, B., & Arismendi, I. (2009). Peces nativos en aguas continentales del Sur de Chile. *Imprenta América Ltda*.

Plew D., Nikora V., Larned S., Sykes J., Cooper G. 2007. Fish swimming velocity variability at constant flow: Galaxias maculatus. New Zealand Journal of Marine and Freshwater Research 41(2): 185–195.

Quaranta, E., Katopodis, C., Comoglio, C. 2019. Effects of bed slope on the flow field of vertical slot fishways. River Research and Applications, 35(6), 656-668.

Quaranta, E., Katopodis, C., Revelli, R., Comoglio, C., 2017. Turbulent flow field comparison and related suitability for fish passage of a standard and a simplified low gradient vertical slot fishway. River Res. Appl. 33, 1295–1305.

Reidy, S. P., Kerr, S. R., & Nelson, J. A. (2000). Aerobic and anaerobic swimming performance of individual Atlantic cod. *Journal of Experimental Biology*, *203*(2), 347-357.

Ruiz-Legazpi, J., Sanz-Ronda, F., Bravo-Córdoba, F., Fuentes-Pérez, J., Castro-Santos, T. 2018. Influencia de factores ambientales y biométricos en la capacidad de nado del barbo ibérico (Luciobarbus bocagei Steindachner, 1864), un ciprínido potamódromo endémico de la Península Ibérica. Limnetica, 37(2), 251-265.

Russon I., Kemp P. 2011. Advancing provision of multi-species fish passage: behaviour of adult European eel (Anguilla anguilla) and brown trout (Salmo trutta) in response to accelerating flow. Ecological Engineering 37: 2018–2024.

Sampaio, F. A. C., Rufino, M. S., Pompeu, P. S., e Santos, H. D. A., & Ferreira, R. L. (2020). Hydraulic flow resistance of epigean and hypogean fish of the family Trichomycteridae (Ostariophysi, Siluriformes). *Subterranean Biology*, *35*, 97.

Sanz-Ronda, F. J., Ruiz-Legazpi, J., Bravo-Córdoba, F. J., Makrakis, S., & Castro-Santos, T. (2015). Sprinting performance of two Iberian fish: Luciobarbus bocagei and Pseudochondrostoma duriense in an open channel flume. Ecological Engineering, 83, 61-70.

Scott, S., Pardo, R., & Vila, I. (2007). Trophic niche overlap between two Chilean endemic species of Trichomycterus (Teleostei: Siluriformes). *Revista Chilena de Historia Natural*, *80*(4), 431-437.

Sfakiotakis, M., Lane, D., Davies, J. 1999. Review of fish swimming modes for aquatic locomotion. IEEE Journal of oceanic engineering, 24(2), 237-252.

Silva, A., Katopodis, C., Santos, J., Ferreira, M., Pinheiro, A., 2012. Cyprinid swimming behavior in response to turbulent flow. Ecol. Eng. 44, 314–328.

Silva, A., Lucas, M., Castro-Santos, T., Katopodis, C., Baumgartner, L., Thiem, J., Aarestrup, K., Pompeu, P., O'Brien, G., Braun, D., Burnett, N., Zhu, D., Fjeldstad, H., Forseth, T., Rajaratnam, N., Williams, J., Cooke, S., 2018. The future of fish passage science, engineering, and practice. Fish Fish. 19, 340–362.

Taguchi, M., Liao, J. 2011. Rainbow trout consume less oxygen in turbulence: the energetics of swimming behaviors at different velocitys. Journal of Experimental Biology, 214(9), 1428-1436.

Trinci G, Harvey GL, Henshaw AJ, Bertoldi W, Heolker F. 2017. Life in turbulent flows: interactions between hydrodynamics and aquatic organisms in rivers. WIREs Water. 4(e1213):1–16.

Tudorache, C., Viaene, P., Blust, R., Vereecken, H., & De Boeck, G. (2008). A comparison of swimming capacity and energy use in seven European freshwater fish species. *Ecology of Freshwater Fish*, *17*(2), 284-291.

Valenzuela-Aguayo, F., McCracken, G. R., Manosalva, A., Habit, E., & Ruzzante, D. E. (2020). Human-induced habitat fragmentation effects on connectivity, diversity, and population persistence of an endemic fish, Percilia irwini, in the Biobío River basin (Chile). *Evolutionary Applications*, *13*(4), 794-807.

Vezza, P., Libardoni, F., Manes, C., Tsuzaki, T., Bertoldi, W., & Kemp, P. S. (2020). Rethinking swimming performance tests for bottom-dwelling fish: the case of European glass eel (Anguilla anguilla). *Scientific Reports*, *10*(1), 1-11.

Videler, J., Wardle, C., 1991. Fish swimming stride by stride: velocity limits and endurance. Rev. Fish Biol. Fish. 1, 23–40.

Videler, J. J. (1993). *Fish swimming* (Vol. 10). Springer Science & Business Media

Vila, I., Contreras, M., & Fuentes, L. (1996). REPRODUCCION DE DIPLOMYSTES NAHUELBUTAENSIS ARRATIA 1987. *Gayana Oceanol*, *4*(2), 129-137.

Vivancos, A., Górski, K., Manosalva, A., Toledo, B., Reid, M., & Habit, E. (2021). Hydrological connectivity drives longitudinal movement of endangered endemic Chilean darter Percilia irwini (Eigenmann, 1927). *Journal of fish biology*, *98*(1), 33-43.

Wang, H., Chanson, H., 2018. On upstream fish passage in standard box culverts: interactions between fish and turbulence. J. Ecohydraul. 3, 18–29.

Wardle, C., 1975. Limit of fish swimming velocity. Nature 255, 725–727.

Watson, J. R., Goodrich, H. R., Cramp, R. L., Gordos, M. A., & Franklin, C. E. (2018). Utilising the boundary layer to help restore the connectivity of fish habitats and populations. Ecological Engineering, 122, 286-294.

Watson, J. R., Goodrich, H. R., Cramp, R. L., Gordos, M. A., Yan, Y., Ward, P. J., & Franklin, C. E. (2019). Swimming performance traits of twenty-one Australian fish species: a fish passage management tool for use in modified freshwater systems. bioRxiv, 861898.

Webb PW (1989) Station-holding by three species of benthic fishes. J Exp Biol 145:303

Webb PW, Cotel AJ. 2010. Turbulence: does vorticity affect the structure and shape of body and fin propulsors? Integr Comp Biol. 50(6):1155–1166.

Webb, P.W., 1988. Steady swimming kinematics of tiger musky, an escociform accelerator, and rainbow trout, a cruiser generalist. J. Exp. Biol. 138, 51–69.

Wilkes MA, McKenzie M, Webb JA. 2017. Fish passage design for sustainable hydropower in the temperate Southern Hemisphere: an evidence review. Rev Fish Biol Fish. 28(1):117–135.

Williams JG, Armstrong G, Katopodis C, Larinier M, Travade F (2012) Thinking like a fish: a key ingredient for development of effective fish passage facilities at river obstructions. River Res Appl 28: 407–417.

CHAPTER 3: ADVANCING MULTI-SPECIES FISHWAY DESIGN FOR SMALL-BODIED FISH SPECIES

This chapter is based on:

Laborde, A. (in preparation)

Advancing multi-species fishway design for small-bodied fish species.

Advancing Multi-Species Fishway Design for Small-Bodied Fish Species

A. Laborde[a]

[a] *Department of Aquatic Systems, Faculty of Environmental Sciences and EULA Centre, Universidad de Concepción, Concepción, Chile*

Abstract

Hydropower plants can severely impact freshwater ecosystems, limiting fish movement. Current fishway design, developed primarily in northern regions, may not be effective in the Southern Hemisphere. Installation of baffles is intended to improve the passage of small-bodied fish species worldwide, but the efficiency of new designs must be tested with a variety of fish assemblies. However, the suitability of fishways to aid upstream movement of small-bodied species has not been tested. This study assessed fish passage performance metrics for *Trichomycterus areolatus*, *Diplomystes nahuelbutaensis* and *Percilia irwini*. They are referred to as the TDP group here and belong to the small-bodied assemblage most exposed to expected hydropower development in Chile. Four 4-metre-long prototype fishways were tested: carpet and unmodified (control), lateral baffles (treatment 1), baffle array (treatment 2), and alternating lateral baffles (treatment 3). Passage of individual fish and interspecific fish groups was assessed during a thirty-minute trial for each prototype. Passage performance was quantified as passage efficiency, percentage of attempts, and percentage of impingement. Despite some individuals being able to swim against high water velocities (> 0.9 m/s^{-1} over 4 m), performance in the control passage was poor. Compared to the control, the treatments involved increased water depth and the creation of heterogeneous flow conditions with low-velocity resting areas. Results show that baffles increased passage efficiency and decreased the percentage of impingements. The lateral baffles configuration (treatment 1) showed the highest passage efficiency for *T. areolatus* (efficiency of 70%, 30% and 0% for treatments 1, 2 and 3, respectively) and *P. irwini* (efficiency of 43%, 0% and 20% for treatments 1, 2 and 3, respectively). In individual and interspecific group experiments, fish passage performance metrics in the lateral baffles configuration were not significantly different for *T. areolatus*, *P. irwini* and *D. nahuelbutaensis*. These findings show that the lateral baffles design, with a group passage efficiency of 37%, could serve as a multi-species fishway to mitigate for impeded upstream movement of *Trichomycterus*, *Percilia* and *Diplomystes*. We conclude that the extent to which understanding fish behaviour and space use to improve fishway design should be explored further.

Keywords: Fish passage, conservation, mitigation, multi-species, small-bodied fish, Chile.

Introduction

Disruption of river connectivity due to instream structures has contributed to the population decline of many fish species around the world (Birnie-Gauvin et al., 2019). The desire to restore river connectivity and establish fish migration pathways through these structures has resulted in the development of fish passages, also known as fishways. This scientific solution relies on the theory of providing additional hydraulic structures to ensure that water velocities and depths are matched with the requirements of the target fish, thus ensuring their physical ability to pass through (Katopodis and Williams, 2012). Various fish passage solution types have been proposed and tested with fish found commonly in northern temperate regions, and particularly with highly prevalent and economically important species (Noonan et al., 2012; Kemp, 2016). Several studies have reported on the flow and turbulence characteristics of conventional fish pass structures, such as vertical-slot (Cardoso, 2015; Hoger, 2015; Quintella, 2015; Ozcan, 2017), pool-weir (Yagci, 2010; Santos et al., 2012; Fuentes-Pérez et al., 2016) and nature-like (Baki et al., 2014; Cassan et al., 2014; Czerny et al., 2015) fishways. A common characteristic of these fish pass structures is that the hydraulic energy is mostly dissipated in an energy cascade process: in vertical-slot fishways the turbulent jets plunge into pools, whereas in nature-like fishways the wake behind the macro-roughness dissipates excess energy. However, research findings and remediation solutions for these species do not necessarily extrapolate to other species due to the high velocity and turbulent kinetic energy (TKE) (Goodrich et al., 2018; Silva et al., 2018). This is particularly true for small-bodied fish, a term that refers to adult fish with a body length of up to 15 cm (Knapp et al., 2019). Small-bodied fish are mainly found in regions of the southern temperate zone, particularly Australia (Watson et al., 2019), New Zealand (Magaju et al., 2020; Dupont, 2020), southern South America (Link et al., 2017; Laborde et al., 2016; Link and Habit, 2015) and Southern Africa (Boubeé et al., 1999; Cussac et al., 2009). A significant lack of information for these species has frequently been noted (Laborde et al., 2016; Franklin and Gee, 2019; Watson et al., 2019). This lack of knowledge of habitat requirements that could inform the design of instream structures or fishways that enable unimpeded passage by small-bodied fish is compounded by pressure exerted by rapid economic expansion and land development (Wilkes et al., 2017; Habit et al., 2018).

The South-Central region of Chile has been generating considerable attention in terms of hydropower exploitation, as it comprises 10 high gradient watersheds with an estimated 12.5 GW potential (Ministry of Energy, 2015), most of which would be supplied by small hydropower plants (SHPs). Central Chile is also part of the Chilean ichthyogeographic province (*sensu* Dyer 2000), a biodiversity hotspot (Myers et al., 2000) accommodating a unique and highly endemic fish fauna. Thus, of major concern are the potential fragmentation of the entire region and the cumulative effects of multiple projects built within the natural range of native species that are predominantly small-bodied and resident (Díaz et al., 2019). This background highlights the need for rapid development of effective bi-directional fishways for Chilean native small-bodied fish species if populations are to survive. With a view to encouraging the development of effective mitigation technologies in Chile, an ecoregion with high endemism, Laborde et al. (2020) developed a methodology to prioritise those assemblages comprising the most prevalent genera occurring at planned project sites. *Trichomycterus*, *Diplomystes* and *Percilia* (the TDP group) were the three genera of small-bodied fish species identified as a starting point for fishway design considering the Chilean target group. However, there are significant gaps in knowledge regarding the systematics, distribution and biology of these freshwater fish (Habit et al., 2006; Vila et al., 2006). In Chile, efforts have been made by Laborde et al. (2016) and Link et al., (2017) to provide hydraulic design criteria for native species.

Evaluation of new designs that are specifically geared towards small-bodied fish are also required (Knapp et al., 2019). Locally confined low-velocity zones are thought to play a significant part in the successful upstream passage of small-bodied fish (Wang et al., 2016; Zhang and Chanson, 2018). Due to their size, small-bodied fish can more readily make use of these smaller flow features. Low-velocity zones should be evenly distributed, continuous, simply providing fish with rest areas along their path upstream (Gerstner,1998). The discharge capacity of a given cross-section is less affected by the inclusion of locally confined low-velocity zones than by an overall reduction in water velocity for a complete cross-section (Zhang and Chanson, 2018). It does, however, lead to increased hydraulic roughness within the wetted surface of a structure (Ead et al., 2002; Baki et al., 2015). Engineering designs of various shapes, forms and arrangements have been developed and used within fishways of different shapes, sizes and lengths (Muraoka et al., 2017; Rodgers et al., 2017; Goodrich et al., 2018; Wang and Chanson, 2018; Amaral et al., 2019; Johnson et al., 2019). The need for effective low-cost solutions to restore habitat connectivity (Kemp and O’Hanley, 2010) has driven the development and testing of new innovative fish passage technologies such as bristle clusters (Montali-Ashworth et al., 2020, 2021), brushes (Kucukali et al., 2016, 2019), mussel-spat ropes (David et al., 2009, 2014), rock ramps (Baudoin et al., 2014; Baki et al., 2016), and different types of baffles: sloping baffles (Newbold et al., 2014), ventilated corner baffles (Cabonce et al., 2018; Sailema et al., 2019), longitudinal square beams (Watson et al., 2018) and other industrial designs (Baker and Boubée, 2006). Bristle clusters have been proposed for gauging weirs, commonly installed to measure river discharge. Although passage efficiency has been assessed in the laboratory for species in vital stages with lengths up to 15 cm, their operation and maintenance in the field can pose challenges (for example, in preventing the spaces between bristles from becoming obstructed). Brush elements were first used in 2002 in Germany (Hassinger, 2015) and approximately 60 brush fishways are currently in operation in Europe. Nevertheless, there are no studies in the literature that have simultaneously examined the flow structure and fish passage efficiency of a brush fishway at the prototype scale, and operational conditions of fish pass structures (i.e., variable headwater and tailwater levels) cannot be accurately simulated (Kucukali et al., 2019). Monitoring data indicate that the brush fishway is not size selective. Furthermore, although ropes were primarily used to improve the passage success of climbing fish species past culverts, a small-scale laboratory trial highlighted their applicability for assisting the passage of a small benthic fish species through otherwise impassable velocity barriers (Tonkin et al., 2012). Although they are size-selective, they have so far been implemented in very gently sloping culverts. The rock-ramp fishway design is well-known. Parasiewicz et al. (1998), DVWK (2002) and USBR (2007) provided practical design guidelines based on the critical velocity criteria for rock-ramp fish passes. Haro et al. (2008) conducted several tests with a field-scale laboratory rock-ramp fishway setup with randomised boulder placement. Cassan et al. (2014) proposed an analytical model to calculate the stage-discharge relationship for a rock-ramp fishway. Baki et al. (2014; 2015) investigated mean flow and turbulence in a rock-ramp fishway with staggered boulders. Baki et al. (2014) developed general correlations for estimating flow depth and velocity from the normalised discharge. As pointed out by Oertel et al. (2011), the concentration, orientation, spacing and pattern of boulders significantly affect the flow in a fishway. Baki et al. (2016) define the effects of channel slope and boulder size and pattern on water level, flow velocity and flow resistance in a rock-ramp fishway to optimise design processes. According to Baker and Boubée (2006), fish ramps containing substratum-roughening elements facilitate passage of two native New Zealand species, namely redfin bullies (*Gobiomorphus huttoni)* and inanga (*Galaxias maculatus)*. Kucukali and Hassinger (2015, 2016) adapted the hydraulic characteristic of a baffle fishway to suit juvenile and small-bodied fish by combining it with a brush fish pass. Roughness elements of the same size and shape have been found to perform differently with arranged changes (Enders et al*.,* 2017). Furthermore, performance for a single species has been found to vary between roughness elements of different types (Amtstaetter et al*.,* 2017). Moreover, there are three main types of baffle fishways that differ due to the installation of the baffles: (1) on the sides only, (2) on the floor and sides, and (3) on the floor only (Larinier, 2002). Finally, due to some of the features identified above and the possibility of altering the baffles design and sizes, baffles passes promise to be the fishway type most suitable for a *TDP* group.

The need to maintain river connectivity for native biota while concurrently preventing or limiting the spread of non-native species has led to a growing interest in developing selective fish passage technologies (Pratt et al., 2009; Rahel, 2013; Rahel and McLaughlin, 2018). There are a few precedents for the use of selective fishways to block the movement of non-native species while allowing native species to pass (Kerr et al., 2020). In Australia, fishways with a dividing wall installed at existing barriers encourage the non-native common carp to jump into a separate compartment, which acts as a trap, while non-leaping native species continue upstream (Stuart et al., 2006). Rahel and McLaughlin

(2018) present a conceptual framework for the development of selective fish passes and highlight the need to rapidly progress this field of research.

Efforts over the past decade to standardise metrics for fishway assessment have increased considerably (Castro-Santos and Haro, 2010; Bravo-Cordova et al., 2021) and there are some examples of meta-data analyses of fishway performance (Bunt et al., 2012; Noonan et al., 2012). These analyses are of great interest in terms of fishway design, although they are still controversial due to the difficulty involved in comparing experiments (Kemp, 2016). The study of passage performance ideally comprises three stages or topics: attraction, entrance and internal passage (Castro-Santos, 2011). Therefore, it is very important to define the specific stage to which the metric refers, or if it covers the overall passage (i.e., including all stages; Bravo-Cordova et al., 2021). Passage efficiency, being one of the most crucial aspects of fishway solutions, is currently the most widely discussed topic in fish passage research (Noonan et al., 2012; Silva et al., 2018). To be effective, a fishway must allow target fish to successfully pass (Baki et al., 2017; Cai et al., 2020). Kerr et al. (2015) defined and tested passage efficiency as the total number of times fish successfully passed as a percentage of total attempts per replicate. They also covered other metrics to measure fish motivation. The passage efficiency of most fish in South America has never been assessed (Agostinho et al., 2002, 2008; Pompeu et al., 2012). Another factor to consider is that fish may abandon an ascent for behavioural reasons rather than due to limits to their swimming ability (Vowles et al., 2019).

The formation of social groups is one of the most striking and familiar aspects of fish behaviour (Godin, 1986; Magurran, 1990; Pitcher and Parrish, 1993; Hoare, 2000). The internal organisation of such groups and the patterns of relationships between their members may differ widely depending on fish species, mode of life, age and motivation, as well as on many biotic and abiotic environmental factors (Pavlov et al., 2000). The term *shoal* is commonly used to refer to any social aggregation of fish, whereas *school* refers more specifically to a synchronized group of fish, typically showing polarised swimming behaviour (Pitcher, 1983; Hoare, 2000).

The suitability of even common baffle designs for small-bodied species assemblages remains untested and minimal data is available on the multi-species passage performance of baffle solutions. Therefore, this study explores the suitability of baffle design in regard to a target group of small-bodied fish species, particularly the TDP group. Passage of *Trichomycterus*, *Percilia* and *Diplomystes* was tested as a study case for a small-bodied target group. Two questions were asked. (1) Which is the baffle design with the highest passage efficiency for small-bodied fish? (2) Does the baffle design with highest passage efficiency work as a multi-species fishway? We began by comparing the passage performance of upstream movement as individuals attempted to pass through a carpet and unmodified (control) fishway and three prototype fishways with different baffle configurations: lateral baffles, baffle array and alternating lateral baffles). The baffle configuration with the highest passage efficiency was identified. We then tested upstream passage performance of the TDP group in the control fishway and in the baffle design with highest passage efficiency. Passage performance in individual and species group experiments were compared.

Methods

Fish collection and maintenance

Trichomycterus areolatus were collected from the Itata River (37°09′56″S, 72°02′06″W, n = 60, mean ± SD total length: 77 ± 1.21 mm, mass: 2.7 ± 1.67 g); and both *Percilia irwini* (n = 60, mean ± SD total length: 54 ± 1.48 mm, mass: 2.0 ± 1.66 g) and *Diplomystes nahuelbutaensis* (n = 40, mean ± SD of total length: 58 ± 0.52 mm, mass: 1.9 ± 0.60 g) from the Biobío River (36°49′10″S, 73°09′52″W). Fish were collected using a backpack electroshocker (Smith-Root LR24, USA) and seine net (2-mm mesh). They were transported in aerated containers to the Hydraulics and Environmental Engineering Laboratory, University of Concepción (< 1 h transport time). There, fish were held in glass aquariums (aerated and filtered, 50% weekly water change to maintain high water quality) at ambient temperature (mean ± SD = 14.1 ± 2.4°C). Trials took place between 15 May and 10 August 2018 and no fish were held for more than two weeks in the laboratory prior to being tested. Mean total length and mean water temperature did not differ between treatments for any genera. To avoid mortality, guidelines for transportation and successful maintenance in captivity of Chilean native fish were followed (Sobenes et al., 2012). Fish were fed ad libitum with live prey (macroinvertebrates from streams and *Enchitrea sp.*, *Tenebrio molitor*, and *Eisenia foetida*) three or four times a week according to Sobenes et al. (2012) and García et al. (2012). Based on Jobling (1982), feeding ceased 48 h before each experiment.

Experimental set-up

Experimental trials were performed in a prototype fishway (5% slope, 4.0 m long, 0.7 m wide and 0.2 m high) (Figure 2a) installed midway along an indoor recirculating flume (10.0 m long, 1.2 m wide and 1.4 m deep) at the Hydraulics and Environmental Engineering Laboratory, University of Concepcion, Chile. The glass walls of the flume allow lateral observation. Discharge was maintained at 10 L/s^{-1} during all trials. The discharge entering the prototype was controlled with a closed-loop control system and considering the frequency of the pump motor based on a fuzzy logic feedback through a programmable logic controller (PLC) and a variable-frequency drive (VFD). The discharge was measured with an orifice plate device installed in the recirculation system with a precision of ± 1%. A carpet substrate was attached to the prototype bottom to increase the roughness. Screens (10 mm square mesh) were fitted downstream and upstream of the prototype to contain fish within the test area.

Under treatment conditions, transversely oriented baffles (152 mm long, 76 mm wide, 34 mm high) were placed on the prototype creating different configurations: lateral baffles (treatment 1), baffle array (treatment 2) and alternating lateral baffles (treatment 3) (Figure 3-1.b, c and d). Baffle height was approximately 0.05 times fishway width (within the recommended range for culverts; Hotchkiss and Frei, 2007). Under treatment 1 (Figure 3-1.b), ten baffles were installed at 30 cm spacing (side to side) at each side of the prototype. Under treatment 2 (Figure 3-1.c), ten baffles were added down the centre, longitudinally interspersed with the existing baffles. Under treatment 3 (Figure 3-1.d), the side baffles were alternately extended (alternating arrows of three blocks either side).

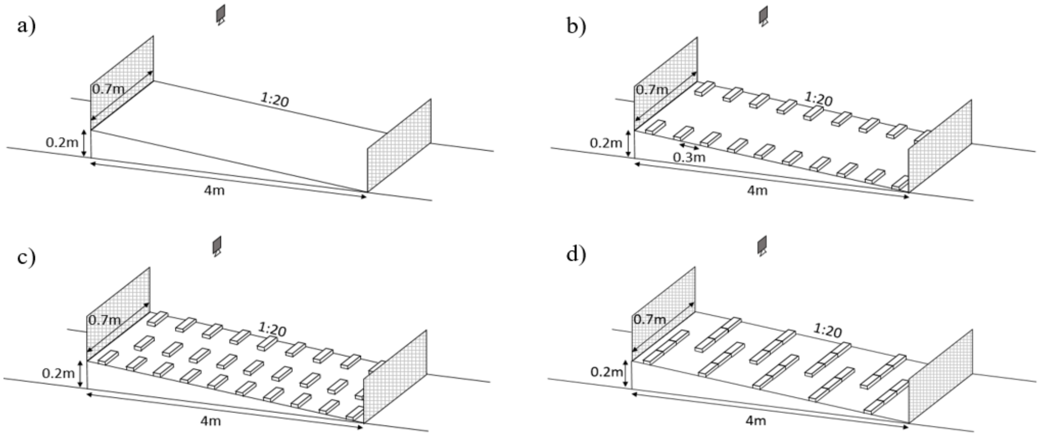


Figure 3-0-1. An experimental prototype fishway used to assess fish passage performance for *Trichomycterus*, *Percilia* and *Diplomystes* under (a) control (carpet and unmodified), and treatments: (b) lateral baffles, (c) baffle array and (d) alternating lateral baffles.

The discharge was selected based on recommendations by Baudoin et al. (2015), who suggest that the minimum water depth, referred to as non-limiting for the successful upstream passage of fish, should be between one and two times the body depth of the fish (e.g., Amaral et al., 2019). In this case, the highest fish body depth was 1.4 cm and discharge created a mean flow depth of 2.9 ± 0.9 cm in the control configuration.

The flow tested in the unmodified and carpet prototype fishway (control) was in the subcritical range (i.e., with a bulk flow Froude number < 1). Flow velocities with ADV could not be measured due to the low water depth. Water depth was measured with a point gauge of 0.1 mm accuracy. Water depth in each baffle treatment was measured along 40 transects perpendicular to the flow (measurement points are shown with dots in Figure 3-2). Due to greater flow homogeneity in the control, measurements were taken at a coarser resolution, at 10 equidistant points along two transects. Flow velocity was calculated for each baffle configuration based on water depth measurements, not including data collected above the baffle face. Flow velocity v (m/s^{-1}) was calculated by $v = Q/A$, where Q is discharge (m^3/s^{-1}) and A is area (m^2); and $A = b \times h$, where b is prototype width (m) and h is cross-section mean water depth (m). Water depth was interpolated between points in ArcGIS (Figure 3-2).

The water depth was 2.9 ± 0.9 cm in the control, 4.6 ± 0.8 cm in lateral baffles (treatment 1), 5.5 ± 1.3 cm in baffle array (treatment 2), and 5.8 ± 1.7 cm in alternating lateral baffles (treatment 3), respectively. The maximum velocities were 0.98, 0.29, 0.32, and 0.34 m/s^{-1} in control and treatments 1, 2 and 3, respectively.

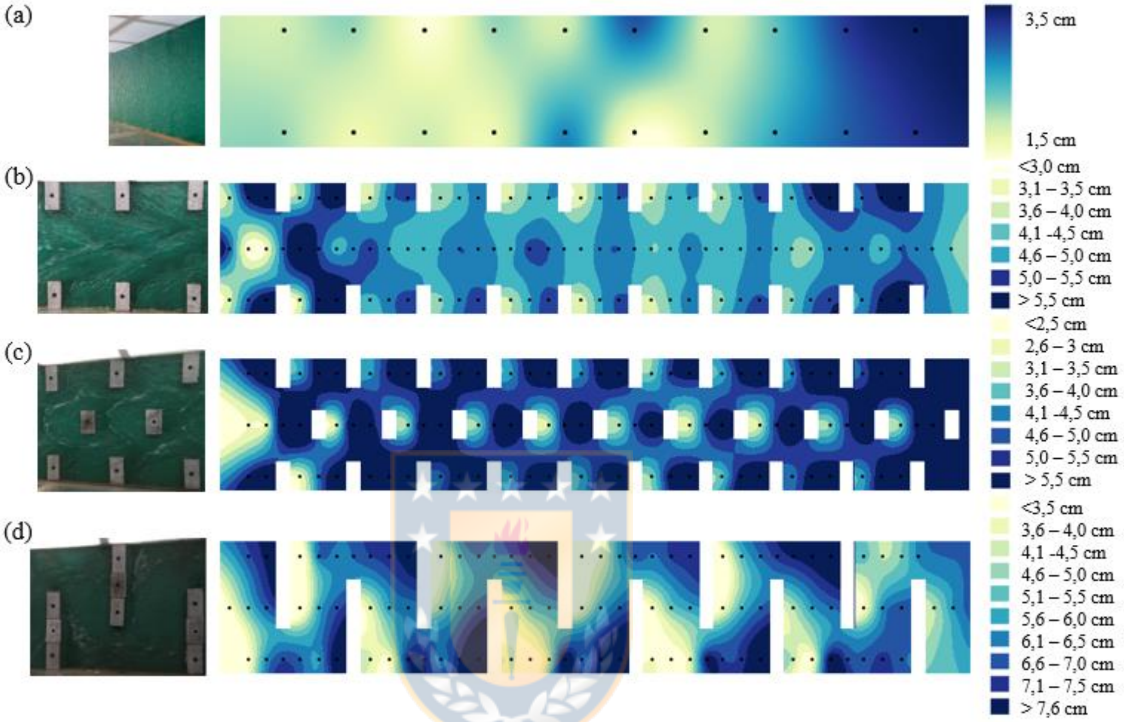


Figure 0-2. Distribution (left) and plan view of the water depth in a 4-metre-long experimental prototype fishway (right), for the (a) control (carpet and unmodified), and treatments: (b) lateral baffles, (c) baffle array and (d) alternating lateral baffles. Water depth was interpolated between points in ArcGIS.

Experimental series and procedure

Passage of *Trichomycterus areolatus* and *Percilia irwini* was evaluated in 10 individual trials (each using a single fish) for each of the four test conditions (control and treatments 1, 2 and 3; total = 40 trials by genera). To answer the question of which of the baffle configurations showed the highest passage efficiency for small-bodied fish, *T. areolatus* and *P. irwini* passage performance metrics were compared for the different baffle configurations. Due to limited availability of *Diplomystes nahuelbutaensis*, species passage was evaluated in 10 individual trials covering only two test conditions (total = 20 trials): control and treatment 1, 2 or 3, whichever showed the highest passage efficiency for *T. areolatus* and *P. irwini*.

To assess TDP group passage performance, passage performance metrics were evaluated in five group trials (of six individuals, each using two individuals by genera), in the two-test condition: control and treatment 1, 2 or 3, whichever showed the highest passage efficiency for *T. areolatus* and *P. irwini* (total = 20 individuals by genera). To answer the question of whether the baffle design with the highest passage efficiency works as a multi-species fishway, species passage performance metrics from individual and interspecific fish group tests were compared for control and treatment 1, 2 or 3, whichever showed the highest passage efficiency for *T. areolatus* and *P. irwini*.

Fish were allowed at least half an hour to acclimatise to flume conditions in a perforated container located 2.5 m upstream of the downstream mesh. A trial began once the container was lifted and the fish were free to move around the experimental area. Trials were ended after 30 min, when a fish successfully reached the upstream end of the prototype, or when a fish became impinged (i.e., when they were unable to escape from the downstream mesh after 3 s). Experiments were completed during daylight hours (8:00-20:00) and fish passage performance was filmed using an overhead Sony Action Cam (HDR AS300, 1280x720 pix resolution and acquisition frequency of 120 Hz). At the end of each trial, the fish was anaesthetised in 2-phenoxyethanol solution (1%) and total length (mm) and mass (grams) recorded. Each fish was tested only once during the study.

TDP group passage performance

Fish passage performance was quantified as (1) passage efficiency; (2) percentage of attempts; and (3) percentage of impingement.

Metric	Description
Passage efficiency	Number of fish that passed through the prototype as a percentage of those that attempted. An **attempt** was identified by a fish drifting back downstream for > 1 s. Any further upstream prototype progression observed was considered a separate attempt as it involved an observable increase in swimming speed to counter high velocity flow. A **pass** occurred when the whole body length of the fish passed the prototype crest.

Percentage of attempts	Number of fish that attempted as a percentage of those tested.
Percentage of impingement	Number of fish that were impinged as a percentage of those tested. An **impingement** occurred when, despite attempts, the fish remain at the downstream mesh for more than 3 s.

Statistical analysis

Assumptions of normality and homogeneity of variance were tested using Shapiro-Wilk tests and Bartlett’s tests, respectively. Due to the low replicate numbers, it was not possible to assess interaction effects.

Fisher’s test was used to assess differences in passage efficiency, percentage of attempts, and percentage of impingement between the control and each baffle configuration, between baffle configurations, and between individual experiments and species group experiments. Statistical analysis was performed in rStudio.

Results

Which is the baffle configuration with the highest passage efficiency for small-bodied fish?

Baffle configurations increased passage efficiency and decreased the percentage of impingements, i.e., fish that drifted and remained at the downstream net (Figure 3-3). In the three treatments, *T. areolatus* and *P. irwini* commonly moved around within the baffle area. *T. areolatus* individuals were very active, using the contours of the baffles to attempt to pass. *P. irwini* individuals were less active, holding position downstream or above the baffles. In some cases, they held position alongside the baffles, mainly prior to an attempt to cross higher velocity zones.

Lateral baffles (treatment 1) were the baffle configuration with the highest passage efficiency for *T. areolatus* and *P. irwini*. Passage efficiency was higher with lateral baffles than in the other baffle configurations for *T. areolatus* (Fisher's exact p = 0.04; efficiency of 70%, 30% and 0% for treatments 1, 2 and 3, respectively) and *P. irwini* (efficiency of 43%, 0% and 20% for treatments 1, 2 and 3, respectively).

In general, the percentage of attempts was high for both genera (above 50%, see Table 3-2). All tested fish actively attempted to negotiate the prototype independent of baffle configuration, except for *T. areolatus* in treatment 3, where the percentage of attempts was significantly lower (Fisher’s exact $p < 0.01$; 60% for treatment 3 versus 100% for treatments 1 and 2).

The percentage of impingements in treatment 1 was lower than in the other baffle configurations (see Table 3-2). In particular, the percentage of impingements was significantly lower in treatment 1 for *T. areolatus* (10%, Fisher’s exact $p = 0.01$) and *P. irwini* (50%, Fisher’s exact $p < 0.01$).

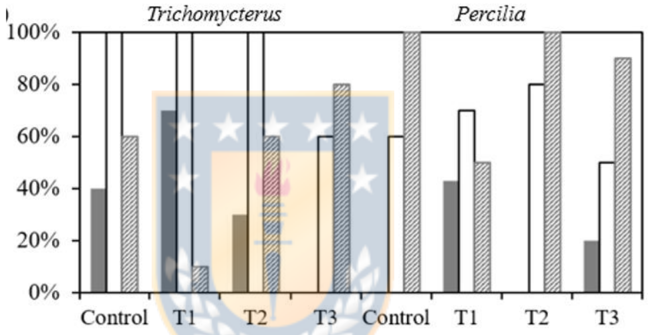


Figure 3-0-3. Summary of upstream passage performance for *T. areolatus* and *P. irwini* during passage through control and three baffle configurations. Solid, clear and hatched bars represent passage efficiency, percentage of attempts and percentage of impingement, respectively.

Table 3-0-1. Fish passage performance metrics (mean value) for *T. areolatus* (T), *P. irwini* (P) and *D. nahuelbutaensis* (D) in individual experiments during passage through a prototype fishway without (control) or with baffle configurations.

Metric	**Genera**	**Control**	**Lateral baffles**	**Baffle array**	**Alternating lateral baffles**
Passage efficiency	T	40%	70% *	30%	0%
	P	0%	43%	0%	20%
	D	0%	10%	-	-
Percentage of attempts	T	100%	100%	100%	60% *
	P	60%	70%	80%	50%
	D	90%	100%	-	-
Percentage of impingements	T	60%	10% *	60%	80%
	P	100%	50% *	100%	90%
	D	100%	70%	-	-

Statistically significant difference by treatment (*).

Does the baffle configuration with the highest passage efficiency work as a multi-species fishway?

Results showed that the passage performance metrics obtained for *D. nahuelbutaensis* follow the same trend described for *T. areolatus* and *P. irwini*. In comparison to the control, the lateral baffles design increases passage efficiency (0% and 10% for control and treatment 1, respectively) and decreases the percentage of impingements (100% and 70% for control and treatment 1, respectively). In species group experiments as in individual tests, individuals were motivated to explore their surroundings. However, under interspecific fish group experiments, when a fish encountered another individual, they generally stayed together, especially when the latter was larger and provided shelter. In these cases, upstream displacement attempts were also motivated by the behaviour of their companions. Fish passage performance metrics in the lateral baffles configuration in both individual and species group experiments were not significantly different for *T. areolatus*, *P. irwini* and *D. nahuelbutaensis*. As such, the lateral baffles design works as a multi-species fishway for small-bodied species. Passage efficiency of the group in the lateral baffles configuration was 37%.

Table 3-0-2. Fish passage performance metrics for *T. areolatus* (T), *P. irwini* (P) and *D. nahuelbutaensis* (D) on individual (Ind) or species Group experiments during passage through a prototype fishway without (control) or with lateral baffles installed.

Metric	**Genera**	**Control**		**Lateral baffle**	
		Ind	**Group**	**Ind**	**Group**
Passage efficiency	T	40%	60%	70%	70%
	P	0%	29%	43%	40%
	D	0%	0%	10%	40%
Percentage of attempts	T	100%	100%	100%	100%
	P	60%	70%	70%	100%
	D	90%	80%	100%	100%
Percentage of impingements	T	60%	40%	10%	30%
	P	100%	80%	50%	60%
	D	100%	100%	70%	60%

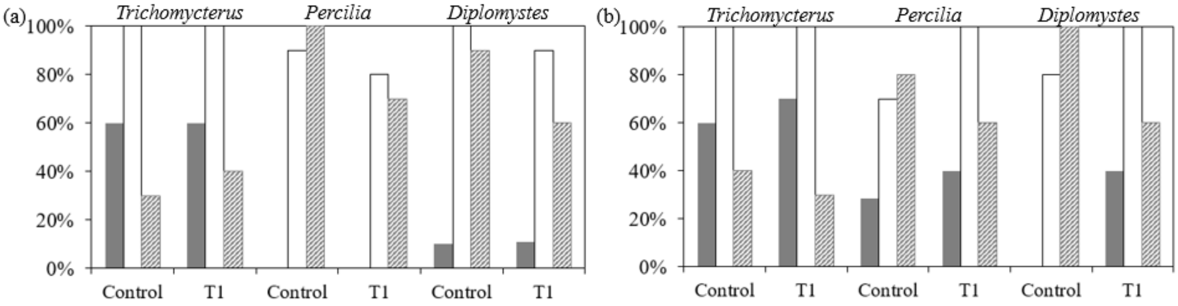


Figure 3-3. Summary of upstream passage performance for *T. areolatus*, *P. irwini and D. nahuelbutaensis* in (a) individuals and (b) species group experiments during passage through control and lateral baffles configurations. Solid, hatched and clear bars represent passage efficiency, percentage of attempts and percentage of impingement.

Discussion

The limited information available on small-bodied fish performance (Franklin and Bartels, 2012; Link and Habit, 2015, Laborde et al., 2016), the lack of understanding of the needs of multiple species worldwide (Branco et al., 2017; Romao et al., 2018) and, in particular, the fact that no mitigation solution is available for Chilean native fish species in the hydropower development context all support the need for development of a multi-species fishway design targeting small-bodied fish species. The suitability of even common baffle designs for small-bodied assemblage groups remains untested and only minimal data is available regarding the multi-species passage performance of these designs. This study explored the suitability of baffle configurations for a target group of small-bodied fish species: the TDP group. Two questions were addressed. (1) Which is the baffle configuration with the highest passage efficiency for small-bodied fish? (2) Does the baffle configuration with the highest passage efficiency work as a multi-species fishway? To answer these questions, we began by comparing the passage performance of individuals as they moved upstream and attempted to pass through a carpet and unmodified (control) and modified prototype (with three different baffle designs: lateral baffles, baffle array and alternating lateral baffles). The baffle design with the highest passage efficiency was identified. We then tested upstream passage performance by species group (TDP group) in the control configuration and in the baffle design with the highest passage efficiency.

Passage performance in individuals and species group experiments were compared.

Lateral baffles were identified as the baffle configuration with the highest passage efficiency. The suitability of a lateral baffles fishway design could be explained by the fact that the simple obstacle distribution creates a simple hydraulic distribution, providing a continuous path that is easily identifiable (Plesinski et al., 2019) and in which hydraulic conditions are highly predictable (e.g., predictable wakes, Lacey et al., 2012; Liao et al., 2003). Swimming behaviours that facilitate this include entrainment, where fish hold position behind a baffle and orient their body based on spatial flow patterns so that the effect of hydrodynamic forces is reduced (Przybilla et al., 2010). Successful fish did not entrain behind the baffles as their movement through the prototype was rapid, but the swim paths recorded suggest a similar energy saving behaviour. Similar mechanisms for velocity reduction have been described in other studies that used roughness elements (e.g., Baker and Boubee, 2006; Hintermann and Hassinger, 2010). According to Lacey et al. (2012), it is likely that a single dominant frequency in flows enhances rather than impedes swimming performance. For example, sculpin (*Cottus pollux*) struggled to pass through a rock-ramp fishway – a nature-like array of roughness elements – when areas of low velocity were not interlinked (Muraoka et al., 2017). Furthermore, several obstacles could limit the existence of a continuous path with suitable hydraulic conditions. This could explain the values of fish performance metrics in baffle arrays. Moreover, even if a continuous path is provided, but the magnitude of the hydraulic conditions encountered by the fish is greater than fish abilities and capacities, it could be a non-physical barrier (Haro et al., 2004). This may be the case of alternating lateral baffles. Passage is compromised above or below these threshold densities, either because fish are unable to manoeuvre between the clusters or because there is insufficient availability of lower velocity areas (Montali-Ashworth et al., 2021).

The lateral baffles configuration could work as a multi-species fishway. Fish passage performance metrics obtained for all genera in both individual and species group experiments were not significantly different and, as such, it is assumed that the presence of individuals of other species does not affect passage performance. Similarities could be explained because *Trichomycterus*, *Percilia* and *Diplomystes* naturally conform to the assemblage (Laborde et al., 2020). In addition, experimental observations revealed the benefits of being in a group. When individuals met, they tended to stay together and motivate the movement of the other. This result is particularly interesting because group displacement has been widely studied for individuals of the same species. Moving in groups can provide both costs and benefits for fish (Krause et al., 2002). Moreover, assessing a particular cost/benefit ratio for any individual is not simple, because it can depend upon its spatial position and hierarchical role in the group, and on its physiological condition (Killen et al., 2012; Marras and Domenici, 2013). A widely acknowledged benefit of group behaviour is the reduction in the cost of locomotion for individuals that trail behind others, taking advantage of vortices (Portugal et al., 2014) or zones of low pressure created by their leading group mates (Marras et al., 2015). Interestingly, this behaviour was observed in *Percilia* as they made attempts behind *Diplomystes* (larger individuals).

Although baffle configurations motivate species to explore their surroundings and to swim upstream, behavioural differences between the species were observed. *Trichomycterus* and *Diplomystes* were highly active and motivated, repeatedly attempting to ascend (i.e., higher percentage of attempts) in comparison to *Percilia*. This could be explained by differences in biological and ecological characteristics of *Trichomycterus* and *Diplomystes* compared to *Percilia* and, hence, could be reflected in different performance (Scott et al., 2007; Piedra et al., 2012; Arratia, 1983; Arratia and Quezada, 2017; Garcia et al., 2012). *Trichomycterus* and *Diplomystes* are naturally more motivated to move, and they are stronger swimmers than *Percilia* (García et al., 2012; Gischke, 2015).

In individual experiments, passage efficiency through the lateral baffles configuration was 70%, 43% and 10% for *Trichomycterus*, *Percilia* and *Diplomystes*, respectively. Similar results were obtained in group experiments (70%, 40% and 40% for *Trichomycterus*, *Percilia* and *Diplomystes*, respectively). Consequently, passage efficiency of the TDP group in the lateral baffles configuration was 37%. This is promising, although it is still well below the 90% efficiency target that Lucas and Baras (2001) recommended as a minimum for sustaining and recovery of populations of diadromous and potamodromous species. Instead, it is closer to the average passage efficiency (48%) recorded in a large meta-analysis by Bunt et al. (2012). Nevertheless, the passage efficiency of the TDP group is similar to that reported for cyprinids through a baffle pass (chub, *Squalius cephalus*, 40%; dace, *Leuciscus leuciscus*, 33%; and roach, *Rutilus rutilus*, 50%) (Armstrong et al., 2010) and for upstream migrating salmonids across all fishway types (mean = 61%; Noonan et al., 2012). Increases in overall passage efficiency from 14% to 80% have also been found for *Galaxias maculatus* and *Galaxias truttaceus* through a culvert following the construction of baffles (MacDonald and Davies, 2007). Evaluation of the performance of fishway structures has indicated that the degree of success achieved can be highly variable and site specific (Kemp, 2012). Indeed, the findings are particularly encouraging, suggesting that the results presented could be adequate considering that they are small-bodied species.

Further research should be done to apply this design to instream structures. Suitable fishway mitigation technologies should not only allow fish to pass through successfully but must also guarantee that energy remains to tackle the challenges faced upstream of the barrier. In this case, the lateral baffles design tested should be 100 m long in order to pass a 5-metre-high structure in the river. It is not possible to extrapolate the fatigue of the tested individuals from a 4-metre to a 100-metre stretch. Moreover, overall fish passage efficiency comprises passage efficiency and a number of other efficiencies. Finally, the ability of the fish to detect the entrance to the structure (i.e., attraction efficiency) must also be considered, along with the capability of those that have detected the entrance to access it (i.e., entrance efficiency). These were not part of the present study and would constitute an interesting focus for additional research in the future.

Conclusions

Current use of fishway designs that may not be effective for small-bodied fish species, combined with the worldwide functional objective of allowing the passage of whole communities, together highlight the need for progress in the design of multi-species fishways for small-bodied fish.

This study explored the suitability of baffle designs for a target group of small-bodied fish species: the TDP group. Two key results are identified: (1) the lateral baffles design shows the highest passage efficiency, and (2) lateral baffles work as a multi-species fishway, as no differences were found between individuals and species groups. Consequently, the lateral baffles design was the most suitable fishway configuration with a passage efficiency of 37% for *Trichomycterus*, *Percilia* and *Diplomystes*.

Further research on small-bodied fish motion and hydraulics focused on how flow influences fish behaviour and vice versa (i.e., ethohydraulics) is needed in order to advance development of suitable designs for small-bodied fish species.

Acknowledgments

The financial support provided by the Chilean Agency for Innovation and Development (ANID) though grant 21160737: “Development of fishways for longitudinal connectivity of Chilean rivers threatened by small hydropower plants”,

and FONDECYT 1150154: “Within watershed barriers and among-watershed leaks: changing connectivity of rivers in central Chile and its impact on native fish” is gratefully acknowledged.

References

Agostinho, A., Gomes, L., Fernandez, D., Suzuki, H. 2002. Efficiency of fish ladders for neotropical ichthyofauna. *River Research and Applications*, *18*(3), 299-306.

Agostinho, A., Pelicice, F., Gomes, L. 2008. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. *Brazilian journal of biology*, *68*, 1119-1132.

Amaral, S., Quaresma, A., Branco, P., Romão, F., Katopodis, C., Ferreira, M., Santos, J. 2019. Assessment of retrofitted ramped weirs to improve passage of potamodromous fish. *Water*, *11*(12), 2441.

Amtstaetter, F., O'Connor, J., Borg, D., Stuart, I., Moloney, P. 2017. Remediation of upstream passage for migrating Galaxias (Family: Galaxiidae) through a pipe culvert. *Fisheries Management and Ecology*, *24*(3), 186-192.

Arratia F. 1983. Preferencias de habitat de peces Siluriformes de aguas continentales de Chile (Fam. Diplomystidae y Trichomycteridae). *Studies on Neotropical Fauna and Environment*, *18*(4), 217-237.

Arratia, G., Quezada-Romegialli, C. 2017. Understanding morphological variability in a taxonomic context in Chilean diplomystids (Teleostei: Siluriformes), including the description of a new species. *PeerJ*, *5*, e2991.

Baker, C., Boubée, J. 2006. Upstream passage of inanga Galaxias maculatus and redfin bullies Gobiomorphus huttoni over artificial ramps. *Journal of Fish Biology*, *69*(3), 668-681.

Baki, A., Zhu, D., Rajaratnam, N. 2015. Turbulence characteristics in a rock-ramp-type fish pass. *Journal of Hydraulic Engineering*, *141*(2), 04014075.

Baki, A., Zhang, W., Zhu, D., Rajaratnam, N. 2017. Flow structures in the vicinity of a submerged boulder within a boulder array. *Journal of Hydraulic Engineering*, *143*(5), 04016104.

Birnie-Gauvin, K., Franklin, P., Wilkes, M., Aarestrup, K. 2019. Moving beyond fitting fish into equations: Progressing the fish passage debate in the Anthropocene. *Aquatic conservation: Marine and freshwater ecosystems*, *29*(7), 1095-1105.

Boubée, J., Jowett, I., Nichols, S., Williams, E. 1999. Fish passage at culverts: a review, with possible solutions for New Zealand indigenous species.

Branco, P., Amaral, S. D., Ferreira, M. T., Santos, J. 2017. Do small barriers affect the movement of freshwater fish by increasing residency?. *Science of the Total Environment*, *581*, 486-494.

Bravo-Córdoba, F., Valbuena-Castro, J., García-Vega, A., Fuentes-Pérez, J., Ruiz-Legazpi, J., Sanz-Ronda, F. 2021. Fish passage assessment in stepped fishways: Passage success and transit time as standardized metrics. *Ecological Engineering*, *162*, 106172.

Baudoin, J., Burgun, V., Chanseau, M., Larinier, M., Ovidio, M., Sremski, W., Voegtle, B. 2015. Assessing the passage of obstacles by fish. *Concepts, design and application. Onema*.

Bunt, C., Castro-Santos, T., Haro, A. 2012. Performance of fish passage structures at upstream barriers to migration. *River Research and Applications*, *28*(4), 457-478.

Cabonce, J., Wang, H., Chanson, H. 2018. Ventilated corner baffles to assist upstream passage of small-bodied fish in box culverts. *Journal of Irrigation and Drainage Engineering*, *144*(8), 04018020.

Castro-Santos, T. 2011. Swimming and other activities: applied aspects of fish swimming performance.

Castro-Santos, T., Haro, A. 2010. *Fish guidance and passage at barriers* (pp. 62-89). Science Publishers: Enfield, NH.

Cussac, V., Fernández, D., Gómez, S., López, H. 2009. Fishes of southern South America: a story driven by temperature. *Fish Physiology and Biochemistry*, *35*(1), 29-42.

Díaz, G., Arriagada, P., Górski, K., Link, O., Karelovic, B., Gonzalez, J., Habit, E. 2019. Fragmentation of Chilean Andean rivers: expected effects of hydropower development. *Revista chilena de historia natural*, *92*(1), 1-13.

Dyer BS. 2000. Systematic review and biogeography of the freshwater fishes of Chile. Estudios Oceanológicos 19: 77–98.

Ead, S., Rajaratnam, N., Katopodis, C. 2002. Generalized study of hydraulics of culvert fishways. *Journal of Hydraulic Engineering*, *128*(11), 1018-1022.

Ead, S., Rajaratnam, N. 2002. Hydraulic jumps on corrugated beds. *Journal of Hydraulic Engineering*, *128*(7), 656-663.

Enders, E., Castro-Santos, T., Lacey, R. 2017. The effects of horizontally and vertically oriented baffles on flow structure and ascent performance of upstream-migrating fish. *Journal of Ecohydraulics*, *2*(1), 38-52.

Franklin, P., Bartels, B. 2012. Restoring connectivity for migratory native fish in a New Zealand stream: effectiveness of retrofitting a pipe culvert. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *22*(4), 489-497.

García, A., González, J., Habit, E. 2012. Caracterización del hábitat de peces nativos en el río San Pedro (cuenca del río Valdivia, Chile). *Gayana (Concepción)*, *76*, 36-44.

Goodrich, H., Watson, J., Cramp, R., Gordos, M., Franklin, C. 2018. Making culverts great again. Efficacy of a common culvert remediation strategy across sympatric fish species. *Ecological Engineering*, *116*, 143-153.

Habit, E., Dyer, B., Vila, I. 2006. Estado de conocimiento de los peces dulceacuícolas de Chile. *Gayana (Concepción)*, *70*(1), 100-113.

Habit, E., García, A., Díaz, G., Arriagada, P., Link, O., Parra, O., Thoms, M. 2019. River science and management issues in Chile: Hydropower development and native fish communities. *River Research and Applications*, *35*(5), 489-499.

Haro, A., Castro-Santos, T., Noreika, J., Odeh, M. 2004. Swimming performance of upstream migrant fishes in open-channel flow: a new approach to predicting passage through velocity barriers. *Canadian Journal of Fisheries and Aquatic Sciences*, *61*(9), 1590-1601.

Jobling, M. 1982. Some observations on the effects of feeding frequency on the food intake and growth of plaice, Pleuronectes platessa L. *Journal of Fish Biology*, *20*(4), 431-444.

Katopodis, C., Williams, J. 2012. The development of fish passage research in a historical context. *Ecological Engineering*, *48*, 8-18.

Kerr, J., Karageorgopoulos, P., Kemp, P. 2015. Efficacy of a side-mounted vertically oriented bristle pass for improving upstream passage of European eel (Anguilla anguilla) and river lamprey (Lampetra fluviatilis) at an experimental Crump weir. *Ecological Engineering*, *85*, 121-131.

Kemp, P. 2012. Bridging the gap between fish behaviour, performance and hydrodynamics: an ecohydraulics approach to fish passage research. *River Research and Applications*, *28*(4), 403-406.

Kemp, P. 2016. Meta-analyses, metrics and motivation: Mixed messages in the fish passage debate. *River Research and Applications*, *32*(10), 2116-2124.

Knapp, M., Montgomery, J., Whittaker, C., Franklin, P., Baker, C., Friedrich, H. 2019. Fish passage hydrodynamics: insights into overcoming migration challenges for small-bodied fish. *Journal of Ecohydraulics*, *4*(1), 43-55.

Kucukali, S., Hassinger, R. 2015. Hydraulic model test results of baffle–brush fish pass. In *Proceedings of the Institution of Civil Engineers-Water Management* (Vol. 168, No. 4, pp. 189-194). Thomas Telford Ltd.

Laborde, A., González, A., Sanhueza, C., Arriagada, P., Wilkes, M., Habit, E., Link, O. 2016. Hydropower development, riverine connectivity, and non-sport fish species: Criteria for hydraulic design of fishways. *River Research and Applications*, *32*(9), 1949-1957.

Laborde, A., Habit, E., Link, O., Kemp, P. 2020. Strategic methodology to set priorities for sustainable hydropower development in a biodiversity hotspot. Science of The Total Environment, 714, 136735.

Lacey, R., Neary, V., Liao, J., Enders, E., Tritico, H. 2012. The IPOS framework: linking fish swimming performance in altered flows from laboratory experiments to rivers. River Research and Applications, 28(4), 429-443.

Larinier, M., Travade, F., Porcher, J. 2002. Fishways: biological basis, design criteria and monitoring. Bulletin Français de la Pêche et de la Pisciculture, (364, spécial milieux tropicaux), 208.

Liao, S. 2003. On the analytic solution of magnetohydrodynamic flows of non-Newtonian fluids over a stretching sheet. *Journal of Fluid Mechanics*, *488*, 189-212.

Link, O., Sanhueza, C., Arriagada, P., Brevis, W., Laborde, A., González, A., Habit, E. 2017. The fish Strouhal number as a criterion for hydraulic fishway design. *Ecological Engineering*, *103*, 118-126.

Link, O., Habit, E. 2015. Requirements and boundary conditions for fish passes of non-sport fish species based on Chilean experiences. Reviews in Environmental Science and Bio/Technology, 14(1), 9-21.

Lothian, A., Gardner, C., Hull, T., Griffiths, D., Dickinson, E., Lucas, M. 2019. Passage performance and behaviour of wild and stocked cyprinid fish at a sloping weir with a Low-Cost Baffle fishway. *Ecological Engineering*, *130*, 67-79.

Magaju, D., Montgomery, J., Franklin, P., Baker, C., Friedrich, H. 2020. A new framework for assessing roughness elements in promoting fish passage at low-head instream structures. *Journal of Ecohydraulics*, *5*(2), 152-164.

Magaju, D., Montgomery, J., Franklin, P., Baker, C., Friedrich, H. 2021. Spoiler baffle patch design for improved upstream passage of small-bodied fish. *Ecological Engineering*, *169*, 106316.

MacDonald, J., Davies, P. 2007. Improving the upstream passage of two galaxiid fish species through a pipe culvert. *Fisheries Management and Ecology*, *14*(3), 221-230.

Marras, S., Domenici, P. 2013. Schooling fish under attack are not all equal: some lead, others follow. *PLoS One*, *8*(6), e65784.

Muraoka, K., Nakanishi, S., Kayaba, Y. 2017. Boulder arrangement on a rocky ramp fishway based on the swimming behavior of fish. *Limnologica*, *62*, 188-193.

Myers, N., Mittermeier, R., Mittermeier, C., Da Fonseca, G., Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853-858.

Newbold, L., Karageorgopoulos, P., Kemp, P. (2014. Corner and sloped culvert baffles improve the upstream passage of adult European eels (Anguilla anguilla). *Ecological engineering*, *73*, 752-759.

Noonan, M., Grant, J., Jackson, C. 2012. A quantitative assessment of fish passage efficiency. *Fish and Fisheries*, *13*(4), 450-464.

Piedra, P., Habit, E., Oyanedel, A., Colin, N., Solis-Lufí, K., González, J., Cifuentes, R. 2012. Patrones de desplazamiento de peces nativos en el Río San Pedro (cuenca del Río Valdivia, Chile). *Gayana (Concepción)*, *76*, 59-70.

Plesinski, K., Gibbins, C., Radecki-Pawlik, A. 2019. Effects of interlocked carpet ramps on upstream movement of brown trout Salmo trutta in an upland stream. Journal of Ecohydraulics.

Pompeu, P., Agostinho, A., Pelicice, F. 2012. Existing and future challenges: the concept of successful fish passage in South America. *River Research and Applications*, *28*(4), 504-512.

Rodgers, E., Heaslip, B., Cramp, R., Riches, M., Gordos, M., Franklin, C. 2017. Substrate roughening improves swimming performance in two small-bodied riverine fishes: implications for culvert remediation and design. Conservation physiology, 5(1).

Romão, F., Branco, P., Quaresma, A., Amaral, S., Pinheiro, A. 2018. Effectiveness of a multi-slot vertical slot fishway versus a standard vertical slot fishway for potamodromous cyprinids. *Hydrobiologia*, *816*(1), 153-163.

Silva, A., Lucas, M., Castro-Santos, T., Katopodis, C., Baumgartner, L., Thiem, J., Cooke, S. 2018. The future of fish passage science, engineering, and practice. *Fish and Fisheries*, *19*(2), 340-362.

Sobenes, C., García, A., Habit, E., Link, O. 2012. Mantención de peces nativos dulceacuícolas de Chile en cautiverio: un aporte a su conservación ex situ. *Boletín de Biodiversidad de Chile*, (7), 27-41.

Habit, E., Dyer, B., Vila, I. 2006. Estado de conocimiento de los peces dulceacuícolas de Chile. Gayana (Concepción), 70(1), 100-113.

Vowles, A. S., Karageorgopoulos, P., Kemp, P. 2019. Upstream movement of river lamprey through a culvert retrofitted with spoiler baffles under experimental conditions. *Journal of Ecohydraulics*.

Wang, H., Chanson, H. 2018. Modelling upstream fish passage in standard box culverts: Interplay between turbulence, fish kinematics, and energetics. *River Research and Applications*, *34*(3), 244-252.

Wang, H., Chanson, H. 2018. On upstream fish passage in standard box culverts: interactions between fish and turbulence. *Journal of Ecohydraulics*.

Wang, H., Chanson, H., Kern, P., Franklin, C. 2016. Culvert hydrodynamics to enhance upstream fish passage: fish response to turbulence. In *Proceedings of the 20th Australasian Fluid Mechanics Conference, AFMC 2016* (pp. 682-1). Australasian Fluid Mechanics Society.

Watson, J., Goodrich, H., Cramp, R., Gordos, M., Franklin, C. 2018. Utilising the boundary layer to help restore the connectivity of fish habitats and populations. *Ecological Engineering*, *122*, 286-294.

Watson, J., Goodrich, H., Cramp, R., Gordos, M., Yan, Y., Ward, P., Franklin, C. 2019. Swimming performance traits of twenty-one Australian fish species: a fish passage management tool for use in modified freshwater systems. *bioRxiv*, 861898.

Zhang, G., Chanson, H. 2018. Three-dimensional numerical simulations of smooth, asymmetrically roughened, and baffled culverts for upstream passage of small-bodied fish. *River Research and Applications*, *34*(8), 957-964.

GENERAL DISCUSSION

Barriers to the movement of fish within river systems are present worldwide. The South-Central region of Chile has been generating considerable attention in terms of hydropower exploitation, as it offers an estimated 12.5 GW potential (Ministry of Energy, 2015), most of which would be supplied by SHPs. The same area is also considered a biodiversity hotspot (Myers et al., 2000), accommodating a unique and highly endemic fish fauna. Thus, of major concern are the potential fragmentation of the entire region and the cumulative effects of multiple projects built within the natural range of native species that are predominantly small-bodied and resident (Díaz et al., 2019). There is a strong need to develop effective fishways for small-bodied Chilean native species. In order to effectively mitigate such extensive longitudinal fragmentation, managers must have suitable mitigation technologies available to facilitate the free movement of fish past barriers. However, technologies capable of re-establishing connectivity for the entire fish community across a range of environmental conditions and past all barrier types do not currently exist (Wilkes et al., 2017; Noonan et al., 2012; Bunt et al., 2012). The experimental research conducted as part of this thesis was undertaken to advance scientific knowledge and aid the development of multi-species fishways for native Chilean species in order to overcome barriers imposed by small hydropower plants (< 5 m in height). The thesis discussed the key findings of this research, including the fundamental knowledge gained, its application to improving fish passage, and the limitations/benefits of results.

Mitigating the impacts of instream structures on fish communities is widely accepted as a critical challenge for their conservation and long-term persistence (Cooney and Kwak, 2013). Target group has expanded from adults of a few species to include whole fish assemblages comprising a diverse range of movement strategies (Mallen-Cooper and Brand, 2007). This was confirmed in chapter one, with most projects being proposed at sites where more than one species is present. The 31 species present in the study area formed a total of 83 assemblages which each comprised up to 13 species (from different genera).

Despite the considerable progress made in the science and management of fish passage in recent decades (Silva et al., 2018), a salmonid-centric focus has neglected the fish-passage needs of other migratory species (Birnie-Gauvin et al., 2018; Lira et al., 2017). Integrated systematic spatial planning and the prioritisation of freshwater conservation efforts is therefore required in order to optimise outcomes (Hermoso et al., 2015). The prevalence of endemic species highlights the biodiversity value of these unique communities (Franklin and Gee, 2018). In chapter one, only species native to the study area were considered. In addition, we indicated their conservation status and whether they were endemic with the aim of prioritising a solution for the species most exposed to hydroelectric development. Of the fish species identified, 74.2% are endemic to the study area, while 38.7% and 48.3% are classified as Endangered and Vulnerable, respectively. The target group, including species of the genera *Trichomycterus*, *Percilia* and *Diplomystes* (the TDP group), encompasses eight species, of which six are endemic. Of particular concern is the situation of *D. nahuelbutaensis*, *D. incognitus* and *P. irwini*. These are endemic to the study area and present at least 49 project sites, making them the species most exposed to expected hydropower development.

Wilkes et al. (2018) have emphasised the need to consider spatial ecological processes in the research and management of fish passage. This need is made evident in chapter one of the present study, in this case at the scale of the species distribution network. Species with the greatest distribution along the river network or concentrated in the upper part of rivers will be the most affected by future hydropower development in Chile as the potential is mainly concentrated in the Andes mountain range and in the Central Valley. In the experiments undertaken in chapter three, the upstream movement of species belonging to the TDP group was assessed at a single barrier. However, river systems are frequently disrupted by multiple barriers which can have cumulative impacts on the proportion of fish that reach lifecycle essential habitat (e.g., Valenzuela et al., 2019; Lucas et al., 2009). Although fish become fatigued after attempting to pass a velocity barrier multiple times (Quintella et al., 2004), there is also evidence that they do not volitionally swim to physiological exhaustion when attempting to traverse a velocity barrier (Haro et al., 2004). Further work is required to ascertain whether the passage efficiency of fish (e.g., TDP group species) through a fishway will be impacted by previous barriers and to establish the minimum recovery time (i.e., distance between barriers) required to mitigate this.

There is often a trade-off between preventing the spread of invasive species and ensuring population connectivity of native species (Jones et al., 2020). In some situations, fishways with shallow water could prove useful to allow the upstream passage of small-bodied native fish yet limit passage of larger invasive species, as shown by Chadderton et al. (2003) with *Cyprinnus carpio* and *Salmo trutta*, which have been identified as species posing a threat to New Zealand's freshwater biodiversity. Similar results are expected for the fishway designs proposed in the present work due to the low water depth.

Katopodis (1994) hypothesises that similar species (i.e., by taxonomic order and families) often display similar swimming performance. Chapter two of the present work provides evidence of the similarity between species of the same taxonomic order and families. However, we note the difference between the trends for species of the same order of small body and larger body sizes. In dimensionless terms, small-bodied individuals have greater endurance than larger individuals. Furthermore, it is important to note that the genera of native species of small-bodied fish worldwide (1) are not the same in different regions (some of them are endemic species), and (2) do not necessarily have representatives of large- bodied fish. Consequently, some analyses performed on small-bodied species can be extrapolated to small-bodied species from other parts of the world, for example, the TDP group (with the taxonomic orders

Siluriform, e.g., *Trichomycterus* and *Diplomystes*, and Perciform e.g., *Percilia*). Nevertheless, for small-bodied endemic species present in only one region of the world, swimming characterisation is necessary. For example, results presented by Laborde et al. (2016) for *Cheirodon galusdae* and *Basilichthys microlepidotus*, belonging to the Characidae and Atherinidae taxonomic orders, are not transferable to other regions due to the absence of the taxonomic order. Results suggest that dimensionless analyses are not transferable to species of the same genus with different body sizes, and generalisation must therefore be limited. Greater availability of data is required to define generalisation limits. Interestingly, dimensionless endurance curves of small-bodied fish species were observed as falling to the right of the same estimated curve of large-bodied fish species of the same taxonomic order. These results suggest that small-bodied fish show higher dimensionless endurance than large-bodied fish. It is possible that this characteristic is part of the evolution of species to allow habitats to coexist.

Frequently, experimental research is undertaken on a scale that is not representative of field conditions (e.g., using small open channel flumes, Servais, 2006; or swim chambers, Tudorache, 2008), a factor that can reduce the applicability of results (i.e., a lack of realism: see Rice et al., 2010). For example, large open flumes allow fish to display more naturally compensatory behaviours (e.g., burst-and-coast swimming) that can influence swimming performance (Tudorache et al., 2007). The absence of these behaviours has been linked with the limited applicability of experimental data obtained in small spaces (Haro et al., 2004). The use of a large open-channel flume during this research enables hydrodynamic conditions and fish behaviour to be assessed at scales relevant to those encountered in the field. For example, small hydropower projects could consider the fishway design proposed in the present work, as the hydrodynamic characteristics created in chapter three are likely to be comparable in terms of magnitude and scale to some barriers found in the field (although this author acknowledges that much larger barriers also exist). For example, the prototype section in chapter three was similar in size to many downstream entrances (e.g., Croze, 2008).

Alternative substrates are available to promote the passage of small-bodied fish species over barriers (see Baker and Boubeé, 2006). The main reason for the effectiveness of these materials is that they increase Manning's N, the roughness coefficient of the ramp (Clay, 1995), which results in a substantial reduction in water velocities and increase in water depths compared to bare or sand ramps. Gravel also creates a range of resting areas where fish of different sizes could be protected from high-velocity flow (Baker and Boubeé, 2006). In the present study, preliminary tests on the acrylic-bottomed step prototype resulted in a high-velocity barrier for all tested individuals. Consequently, a carpet bottom was incorporated to increase roughness, and water depth was increased.

Increasing the roughness coefficient of the fishway through baffling may be effective in decreasing water velocities but can result in increased turbulence and shear stress, which are also known to affect the passage performance of fish species (Haro and Kynard, 1997; Pavlov et al., 2000; Lupandin, 2005; Silva et al., 2012). In chapter three we demonstrated that the incorporation of baffles in the prototype fishway effectively increased passage efficiency and the percentage of attempts, and decreased the percentage of impingements, demonstrating that it constitutes a suitable fishway configuration for small-bodied fish species. In addition, three different baffle configurations were evaluated (lateral baffles, baffle array and alternating lateral baffles), and lateral baffles were identified as the most suitable for the TDP group.

In some cases, the incorporation of fishways has led directly to the recovery of upstream fish communities (Marques et al., 2018), particularly for diadromous species on low-head barriers (Amtstaetter et al., 2017; Rourke et al., 2019). However, in other cases, fishways have not enabled adequate passage rates to support population recovery (Agostinho et al., 2007; Brown et al., 2013). In chapter three, the passage efficiency of the lateral baffles configuration was quantified for the first time for an assemblage of small-bodied fish species. The efficiency for the TDP group was 37%. This is promising, although it is still well below the 90% efficiency target that Lucas and Baras (2001) recommended as a minimum for sustaining and recovery of populations of diadromous and potamodromous species. Instead, it is closer to the average passage efficiency (48%) recorded in a large meta-analysis by Bunt et al. (2012). Nevertheless, the passage efficiency of the TDP group is similar to that reported for cyprinids through a baffle pass (chub, *Squalius cephalus*, 40%; dace, *Leuciscus leuciscus*, 33%; and roach, *Rutilus rutilus*, 50%) (Armstrong et al., 2010) and upstream migrating salmonids across all fishway types (mean = 61%; Noonan et al., 2012).

For fish to successfully negotiate a fishway, they must be able to, first, approach the fishway; second, locate and enter the fishway entrance; third, ascend the full length of the fishway; and fourth, exit the fishway (Stuart and Mallen-Cooper, 1999). The present research involved experiments to assess the third aspect, namely the percentage of fish able to ascend the full length of the fishway (i.e., passage efficiency) (Stuart and Mallen-Cooper, 1999; Stuart et al., 2008).

Additionally, the energetic cost of passage may leave fish with insufficient energy reserves to reproduce or complete other basic life functions (Caudill et al., 2007; Thiem et al., 2016). There are also clear implications for the provision of resting pools in fish pass design, which are added in an effort to prevent fatigue (Katopodis, 1992; Castro-Santos and Haro, 2010; Williams et al., 2012). If flow velocitys within resting pools are not sufficiently low, fish may be unable to negotiate other parts of the fish pass (Castro-Santos and Haro, 2010).

Excessive turbulence has been implicated as a key factor hindering effective fish passage at mitigation structures designed to improve connectivity in anthropogenically fragmented rivers (Bunt et al., 2000; Mallen-Cooper and Brand, 2007; Foulds and Lucas, 2013). This is presumably because it can increase energetic expenditure (Enders et al., 2003; 2004; 2005) and, if of an equivalent scale to fish length, can reduce stability (Tritico and Cotel, 2010). However, it has also been suggested that the judicial use of turbulence could enhance fish passage (Castro-Santos et al., 2009). The literature review highlighted that upstream fish passage research will benefit from a better understanding of the fundamental principles of how fish utilise complex flows (Castro-Santos et al., 2009) and of the hydrodynamic metrics that are most appropriate from a biological perspective to describe those flows (Lacey et al., 2012; Vowles et al., 2013). However, although information on the range of hydrodynamic conditions under which fish can express specialised behaviours is beginning to accumulate (e.g., Akanyetiand Liao, 2012; Vowles et al., 2015; Kerr et al., 2017), further work is required, especially for small-bodied fish species.

GENERAL CONCLUSIONS

The general objective of this thesis was to evaluate a multi-species fishway design to allow native Chilean fish species to overcome barriers imposed by small hydropower plants (< 5 m in height).

The lateral baffles fishway design provides a solution to longitudinal river fragmentation for the TDP group, the assemblage potentially most affected by hydropower development in Chile.

The main conclusions are:

Assemblages of native Chilean fish vulnerable to extensive hydropower development were identified. Following a proposed strategic methodology to set priorities for sustainable hydropower development in a biodiversity hotspot, three categories of project were identified according to their need for mitigation technology, namely project sites where mitigation is (1) not required (15%), (2) required and considered feasible (35%), and (3) required but considered challenging (50%). The most frequent genera in the different assemblages were *Trichomycterus*, *Diplomystes*, and *Percilia*, referred to as the TDP group. A total of 87 projects were planned at sites where only species belonging to the TDP group were present.

Based on the morphometric characterisation of the species belonging to the TDP group, species with similar characteristics and endurance information were identified. Dimensionless endurance was applied for *Trichomycterus*, *Percilia* and *Diplomystes*. Consequently, expected distance design curves as proposed by Peake (1997) were estimated.

The suitability of baffle designs for a target group of small-bodied fish species (the TDP group) was explored. The lateral baffles configuration showed the highest passage efficiency of the three baffle designs (above baffle array and alternating lateral baffles). Moreover, lateral baffles work as a multi-species fishway because no difference was found between individuals and interspecies group. Consequently, the lateral baffles design was the most suitable fishway configuration with a passage efficiency of 37% for *Trichomycterus*, *Percilia* and *Diplomystes*.