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Quantifying links between instream woody habitat and freshwater fish species in south-eastern Australia to inform waterway restoration

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ABSTRACT

1. Removal of instream woody habitat (IWH) is one factor attributed to declines in fish populations worldwide. Restoration of IWH to help fish populations to recover is now common; however, quantitative predictions about the outcomes of these interventions is rare. As such, quantitative links between IWH and fish abundance is of interest to managers to inform conservation and restoration activities.
2. Links between instream habitat attributes, especially IWH, and selected fish species of recreational, cultural, and ecological significance were explored at 335 sites spanning eight streams across south-eastern Australia. Data were collected on fish abundance and length, IWH density and a range of other habitat attributes at a scale that incorporated at least one of each of the major mesohabitat types (functional river elements). The data were analysed using Bayesian hierarchical generalized linear mixed models to examine fish habitat associations and used to make quantitative predictions of responses to future restoration.
3. Strong positive relationships were found between fish abundance and IWH density and the strength of this relationship varied between species and waterways. Murray cod (*Maccullochella peelii*), a species commonly targeted by IWH interventions, displayed the strongest association with IWH density. River blackfish (*Gadopsis marmoratus*) showed a significant relationship with IWH, but this effect was waterway-specific. These results may reflect differences in the life histories of these two species. Fish length was only related to IWH for river blackfish. We suggest that

differences in habitat association through ontogeny may be more relevant at smaller spatial scales.

4. The results generated in this study can be used to guide waterway restoration and develop quantitative predictions about how fish might respond to IWH interventions across south-eastern Australia. This approach provides a powerful quantitative framework within which to explore management options and objectives, and to test our predicted responses to habitat restoration.

Key words: stream, river, habitat management, ecosystem services, restoration, abstraction,

1. INTRODUCTION

Freshwater biodiversity is threatened by a range of disturbances that broadly encompass flow modification, over-exploitation, water pollution, species invasions, and habitat degradation that threaten freshwater fish biodiversity (Vörösmarty et al., 2010; Dudgeon et al., 2006). One major way that humans have damaged habitats is by removing instream woody habitat (IWH; Kitchingman, Tonkin, & Lyon 2013) to improve boat navigation, prevent floods, and mitigate erosion (Abbe & Montgomery, 1996; Brooks, Gehrke, Jansen, & Abbe, 2004; Chin et al., 2014). IWH is important for many fish species, providing substrate for food resources, refuges from competitors and predators, spawning habitat, and shelter from flowing water (Jackson, 1978; Rowland, 1998; Crook & Robertson, 1999; Howson, Robson, Matthews, & Mitchell, 2012). These reductions in IWH are therefore a likely contributing factor to the observed declines in freshwater fish abundance and distribution in highly modified rivers (Crook & Robertson, 1999; Brooks et al., 2004; Erskine, 2015).

In view of its value for fish, and for other ecological and geomorphological reasons (Wohl et al., 2019), restoring wood to waterways is a major activity for waterway rehabilitation. IWH is one of the most common and oldest river rehabilitation techniques, and many methods developed in the north-eastern USA during the 1920s and 1930s have undergone continual refinement and are still in use today (Roni & Beechie, 2013; Thompson & Stull, 2002; Roni, Beechie, Pess, & Hanson, 2015). As much as 38% of stream restoration projects in the US relate to instream structural habitat and these have provided valuable information and guidance for IWH restoration (Palmer, Hondula, & Koch, 2014).

Effective restoration requires planning and goals that are informed by knowledge about the likely ecological responses, the spatial and temporal scales over which they occur, and the causal pathways involved (Palmer et al., 2005; Howell et al., 2012). If IWH restoration, or any intervention more generally, is aimed at producing a biotic response, such as increasing the abundance of native fish, then the first step is to understand associations between the target species and habitat variables (Bond & Lake, 2003). This information can help set realistic goals for a range of species (i.e. which species are likely to respond and when), which in turn can guide monitoring so that sampling is completed at appropriate intervals relative to the timing of expected responses. Importantly, it will help set realistic expectations about how species respond over long time-frames. Although fish are likely to respond to the addition of wood, it may not benefit all species or ontogenetic stages (Langford, Langford & Hawkins, 2012). Thus, knowledge of species-specific associations with IWH densities and distributions across various spatial scales is needed to help maximize the effectiveness of IWH restoration (Howson et al., 2012) and fish conservation.

The spatial scale of fish responses is a particularly important consideration for IWH restoration. The relationship between fish and IWH at small spatial scales is well demonstrated (Lehtinen, Mundahl, & Madejczyk, 1997; Roni & Quinn, 2001; Wright & Flecker, 2004). For example, fish diversity, distribution and abundance (especially of salmonids in the northern hemisphere) has been positively associated with IWH through the provision of critical mesohabitats such as increasing pool area and diversity of hydrodynamic conditions (House & Boehne, 1986; Bisson, Sullivan, K., & Nielsen 1988; Cederholm et al., 1997; Rosenfeld, Porter, & Parkinson, 2000; Roni et al., 2015). Similarly, positive associations have been well documented at micro-habitat scales whereby attributes of IWH enhance essential population processes such as spawning (Bustard & Narver, 1975; Crook & Robertson, 1999; Nicol, Lieschke, Lyon, & Koehn, 2004) or provide refuge from extreme water velocities (Fetherston, Naiman, & Bilby, 1995; Gippel, 1995; Abbe & Montgomery, 1996).

Comparatively less is known about whether these positive associations between fish and IWH extend beyond micro- and mesohabitat scales to influence fish distribution and abundance at river reach, segment or network scales (Wondzell & Bisson, 2003). Some studies conducted at a whole-reach scale report positive relationships between fish abundance or distribution and IWH density (Stewart, Bayliss, Showler, Pullin, & Sutherland, 2006; Lyon et al., 2019) but often weaker results have been observed (Wondzell & Bisson, 2003; Roni, Hanson & Beechie, 2008; Schmutz et al., 2014; Hering et al., 2015). For example, Lyon et al. (2014) reported a whole river-reach increase in the abundance and biomass of Murray cod *Maccullochella peelii* following a large-scale IWH reintroduction programme in the Murray River, Australia but this response was not consistent for several other native species that display strong associations with IWH at microhabitat scales. The weaker responses often observed at larger scales may occur for a number of reasons. First, other stressors, such as altered hydrology may also mask the local-scale effects of habitat enhancement at these larger scales (Wahl, Neils, & Hooper, 2013). Second, either the spatial scale of monitoring (Kail & Wolter, 2013; Wolter, Buijse, & Parasiewicz, 2016), or the restoration effort may not match the requirements of the target species (Hering et al., 2015). Third, fish habitat associations might be stronger at particular spatial scales, and the scale at which a study is focused may determine the strength of the habitat associations that are observed (Hale, Colton, Peng, & Swearer, 2019). It may often not be appropriate, therefore, simply to assume that relationships observed at smaller scales will automatically 'scale up' to larger spatial extents, and empirical data are needed at both small and large scales.

To help guide future IWH restoration efforts, links between IWH and fish species in Victoria, south-eastern Australia were investigated. Reductions in IWH in south-eastern Australia are likely to have contributed to declines in fish populations (Tonkin et al., 2016), with more than half the 46 native freshwater fish species in the Murray-Darling Basin listed as threatened or of conservation interest (Lintermans, 2007). Large quantities of IWH were still being removed from rivers until the late 1980s (Murray-Darling Basin Ministerial Council, 1987), so IWH restoration in Australia has a short history, with trials only commencing in the late 1990s (Brooks et al., 2004; Bond & Lake, 2005; Scealy, Mika, & Boulton, 2007). Given the drastic reduction of IWH and the high numbers of species of conservation concern, the potential benefits of IWH restoration are high.

Relationships between IWH density and fish were examined for several species of high recreational, cultural or ecological significance in Australia that are often targeted by IWH works. Strong relationships between IWH and some of the focal species have been demonstrated at micro- and mesohabitat spatial scales (e.g. Murray cod, Koehn, O'Connor, & Jackson, 1994; Nicol et al., 2004; Koehn, 2009; and river blackfish *Gadopsis marmoratus,* Koehn et al., 1994; Koster & Crook, 2007; Howson et al., 2012). Relationships between fish and IWH density were explored at scales that incorporate at least one of each of the major mesohabitat types (functional river elements such as pools and riffless), both in terms of fish abundance but also length, as fish habitat requirements may differ through ontogeny (Schlosser, 1991; Turschwell, Balcombe, Steel, Sheldon, & Peterson, 2017). The results at this larger scale were compared with those that have observed relationships between fish and IWH at smaller scales, and used to help guide monitoring of future restoration efforts.

2. METHODS

2.1 Study area and site selection

The state of Victoria in south-eastern Australia covers approximately 227,600 km^2, with watercourses varying in geomorphology, hydrology and flora and fauna (VRHS, 2002; Kitchingman et al., 2016). Waterways across the state were still being subject to extensive riparian clearing and direct removal of large quantities of IWH as recently as the mid 1980s (Murray-Darling Basin Ministerial Council, 1987), with reductions in IWH density predicted to range from 20–95% (Tonkin et al., 2016). Eight waterways were selected of varying stream size, altitude, and fish community structure. Importantly, these stream types and fish species therein are frequently targeted as beneficiaries of IWH restoration (see Supporting Information, Table S1 for a species list; Figure 1). Sites within waterways were then selected to reflect the diverse array of habitat conditions within each waterway including IWH, riparian vegetation overhang and water depth, based on previous habitat assessments and aerial imagery (Tonkin et al., 2016). For each waterway, sites were selected within reaches (as described in Ladson et al., 1999) that have similar geomorphological and hydrological attributes. This accounted for the influence of landscape scale drivers such as river flow on fish distribution (Bond, Thomson, Reich, & Stein, 2011), thereby increasing our ability to identify the importance of other habitat associations. The length of each site was chosen to include at least one of each of the major mesohabitat types (functional river elements; Wolter et al., 2016) within the site, and generally increased with increasing waterway width. For example, a site within an upland zone encompassed pools, riffles and runs (mean length generally < 110 m; Supporting information, Table S1), and lowland floodplain sites included beaches, outer bends and backwaters (mean length generally > 100 m; Supporting information, Table S1). As such, the sites reflected a 'sub-reach' scale, containing each of the major mesohabitat types from within the reach, while still keeping reach-scale attributes such as hydrology, which also influence fish populations, relatively constant.

2.2 Fish surveys

Single-pass electrofishing was used to survey each of 335 sites spanning the eight waterways (Table S1). Each site was spatially defined by the wetted area (m^2) at the toe-of-bank. All wetted, accessible habitats within the channel were surveyed between the pre-defined start and end points upstream and downstream. Larger waterways were sampled using electrofishing vessels fitted with a Smith Root® model 5 Kva generator powered pulsator (GPP), while the smaller, shallower waterways were sampled using backpack electrofishing equipment (Smith Root® Model 20). Each waterway was sampled with a single gear type. Electrofishing effort (total power on, time in seconds) and distance fished were recorded for each site. To minimize the effect of changing river levels on electrofishing efficiency, surveys were undertaken during periods of low river levels that generally coincided with summer or early autumn for unregulated waterways, or late autumn and early winter for regulated waterways (the period of minimum irrigation transfers). This timing also reduced any uncertainty associated with seasonal variation in fish distribution, as surveys were conducted outside of the known spawning period of these potamodromous species and associated movements related to spawning). All fish captured were identified, counted and their total length (mm; regardless of caudal fin shape) and weight (nearest gram for priority species only) recorded (Supporting Information, Table S1).

2.3 Instream habitat variables

Although this study focused on IWH, a range of other habitat variables were also measured, just before or immediately following fish surveys:

2.3.1 Instream woody habitat

IWH data were collected following Kitchingman et al., (2013) whereby individual IWH masses were spatially located along the wetted region of the site, and their estimated size and complexity were recorded using a Trimble® GeoExplorer® XT6000 series handheld Global Navigation Satellite System coupled with a laser range finder. Where appropriate, a Humminbird 998cx SI side scan sonar was also used to locate fully submerged IWH. Size and complexity were measured and converted to volume (m^3). IWH data were generally collected in the days or weeks prior to fish surveys as IWH can sometimes show considerable temporal variation.

The total IWH volume calculation for each site was then divided by the site toe-of-bank area (most representative of the wetted surface area) to produce a standardized wood volume density (m^3m^{-2}; Tonkin et al., 2016). To gain insight into the importance of the complexity of IWH for fish, a metric of the area of complex IWH was also generated. Specifically, only IWH with a complexity category of 4 (≥4 stems) was included, and the area value was taken from the lower area of the size bracket (i.e. 1-5m^2 = 1m^2; >5-10m^2 = 5m^2; >10-20m^2 = 10m^2; >20m^2 = 20m^2). Descriptions of habitat complexity and size parameters followed those of Kitchingman et al. (2016). The areas of all IWH structures were summed per site then divided by the site area.

2.3.2 Riparian overhang

Riparian vegetation overhang was measured along the entire Index of Stream Condition (ISC) network in 2010 and 2011 using LiDAR (light detection and ranging) remote sensing technology (Wilson, 2013). The ISC is a functional management scale used for assessing stream condition across the state of Victoria. A standardized riparian vegetation overhang metric was generated. The area of riparian vegetation overhang for the wetted area within 5m of the bank at each site was calculated and expressed as a percentage of the site's entire wetted area within 5m of the bank.

2.3.3 Other structural habitat

The presence of other structural habitat (binary) including expanses of rock (including rock banking), live tree root masses, and undercut banks was recorded at each site, because it provides a similar ecological role to IWH (particularly at the micro-habitat scale).

2.3.4 Water depth

Within each site, water depths were measured during fish sampling and IWH data collection. Water depths were estimated after sampling when data were collected on foot. When collecting data by boat, water depths were recorded using the Hummingbird 998cx SI side scan sonar. The data were then summarized into mean and maximum values for each site.

2.3.5 Bank width

Bank width was measured at transects of the toe-of bank, spaced every 25m throughout the entire ISC network in 2011 (Wilson, 2013). Using these data, the average bank width was calculated for each site (standardized for a given waterway). Bank width and water depth data per site provide insight about water velocity; sites observed with increased water velocity were relatively narrow and/or shallow. Bank width and water depth were used as surrogates to help interpret the influence of water velocity on fish distribution and abundance, as velocity was not measured directly.

2.4 Data analysis

All analyses were conducted on data collected for the priority fish species given their cultural, conservation or recreational value, and are frequently targeted by IWH restoration: Murray cod *Maccullochella peelii*, trout cod *Maccullochella macquariensis,* golden perch *Macquaria ambigua*, river blackfish *Gadopsis marmoratus*, Macquarie perch *Macquaria australasica*, two-spined blackfish *Gadopsis bispinosus*, brown trout *Salmo trutta* and two-spined blackfish *Gadopsis bispinosus* (see Supporting Information, Table S1). Bayesian generalized linear models (GLMs) were used to explore the relationships between fish abundance and length (mixed model; GLMM) and environmental predictors. Potential collinearity between predictors was initially explored (graphically and using pairwise correlations); IWH density and complexity were highly correlated (correlation co-efficient = 0.63 to 0.94 across waterways) so only the former was included. It was not possible to run a global model (i.e. include all species) as the level of overdispersion differed between species, and species composition differed between waterways, so separate models were run for each species: an abundance model and a fish size model.

For the models of fish abundance for each species, the number of fish caught was the response variable, and electrofishing distance (log-transformed) was added as an offset to adjust for variable sampling efforts (catch per unit effort; CPUE). A negative binomial error distribution was assumed for these models. The second model ensemble was fitted with individual fish length as the response variable (log-transformed), assuming a Gaussian error distribution. Both sets of models then included the habitat complexity measures: IWH density (continuous), vegetative overhang (continuous), and the presence of non-IWH (categorical). River was also included as a fixed effect as well as the two-way interactions between river and IWH density to determine whether the effect of density differed across rivers for each species, and between river and vegetation type. To control for other potential factors that affect CPUE estimates (either through altering detection efficiencies or actual fish densities), average river width and average site depth for each site were included. IWH density was log-transformed to reduce leverage effects of high IWH density observations. To account for possible linear spatial patterns along each waterway, an interaction between distance along the river from the most downstream site and river (separate slopes) was included. The fish length model included a random effect for site.

For all models, a posterior hypothesis testing was performed to check whether the average IWH density across all waterways differed from zero. The average IWH density slope was computed by estimating the IWH density slope for each river and then obtaining the average of those slopes (and its uncertainty) using the posterior distributions. In addition, a subsequent model was run without the interaction and the two models were compared using the Widely Applicable Information Criteria (WAIC) to determine if the interaction improved the model fit. For all models, the model with the interaction was selected as the best model. All continuous variables were z-transformed for the analysis to standardize the resulting regression coefficients. Significant effects were defined if the 95% credible interval for an estimate did not overlap with zero.

Noninformative priors were used for all estimates and model convergence for all parameters as indicated by Gelman-Rubin statistics < 1.01 (Gelman, Carlin, Stern, & Rubin, 2004). Model fit was assessed through residual analysis as well as how well the raw data aligned with predicted values from the model (posterior predictive checks). Remaining spatial autocorrelation in the residuals was examined using Moran's I with a distance matrix that assumed that different rivers were independent, and none was found (all Moran's I had $P >$ 0.1). All models were run in R (R Development Core Team, 2016 v3.2.4) with the brms package (Bürkner, 2017).

3. RESULTS

3.1 Fish abundance model

On average across all waterways, CPUE for all species was positively related to IWH density, although *M. ambigua* and *S. trutta* did not achieve significance (Figure 2; Supporting information, Table S2). Estimates for the IWH density effect were similar across the species, except for trout cod *M. macquariensis*, which had a much larger effect with larger variability. For all species (except *M. ambigua* which was only found in one river), the model with the interaction between waterway and IWH density was a better fit, indicating that waterways differed in the effect of IWH density. These river effects were largest in *M. macquariensis* which mostly explained the large variation in the average IWH density effect (Figure 2).

To assess graphically whether some waterways showed consistent patterns, individual river slope estimates from each species model were calculated (Figure 3; Figure 4). The Goulburn R. showed consistent increases in CPUE with IWH for three species (Figure 3; Figure 4). Shepherds Ck. was the only site in which the IWH slopes showed no effect (based on the 95% CIs overlapping with zero for both species; Figure 4). When relationships between CPUE and IWH density were detected for particular waterways and species, generally the strongest relationships (i.e. areas where the slope of the model are most pronounced) were when both CPUE and IWH density were lowest (Figure 3).

Vegetation overhang was associated with decreased CPUE for *M. macquariensis* (Supporting information, Table S2, Figure 2b). For non-IWH, *G. marmoratus* and *M. australasica* CPUE had a significant decrease (~40% to ~50% decrease) when other structural habitat was present

(Supporting information, Table S2). *Maccullochella macquariensis*, *M. peelii*, and *S. trutta* had lower CPUE rates as average water depth increased. CPUE for *M. australasica* increased with increasing water depth (Supporting information, Table S2).

3.2 Fish length model

There was no general effect of IWH density, vegetation slope or non-IWH on fish length response across any of the species (Supporting information, Table S3; Figure 5). Only for *G. marmoratus* and *M. australasica* was the model with an interaction between river and IWH selected as the better model, although only *G. marmoratus* had a significant IWH slope indicating that fish length decreased with increasing IWH (Supporting information, Table S3). As with the fish abundance, there were large confidence intervals for the *M. macquariensis* estimates and hence little information on a potential effect.

The only factors that explained some length variation were river and river average depth (Supporting information, Table S3). Average length varied across rivers for *G. marmoratus* and *M. peelii*. Average length increased with average depth for *G. marmoratus* and *M. australasica* (Supporting information, Table S3).

4. DISCUSSION

Strong positive relationships between targeted fish species and IWH density were found using data collected across a broad spatial scale, encompassing more than 300 sites spanning eight waterways. These results are consistent with previous empirical studies and conceptual reviews demonstrating links between IWH and fish populations (Gregory, Boyer, & Gurnell, 2003; Howell et al., 2012; Roni et al., 2015). Although these links have been demonstrated to operate over a range of spatial scales from microhabitats (e.g. Howson et al., 2012) to entire river basins (Reeves, Everest, & Sedell, 1993), few studies in the southern hemisphere have focused on relationships at the larger end of this spatial range (but see Lyon et al., 2019).

The strength of the relationship between fish abundance and IWH varied between species and waterways. The most consistent responses were observed for Murray cod *M. peelii*, a species that is associated with IWH at micro- and meso-habitat scales (Koehn et al., 1994; Nicol et al., 2004; Boys & Thoms, 2006; Koehn, 2009) and is a common focal taxon for IWH interventions in southern Australia. Recently, Lyon et al., (2019) demonstrated a positive reach-scale response by this species following a large-scale IWH intervention programme on the Murray River. Conversely, we found the strength and direction of relationships was more variable for other species, showing that fish–habitat associations may be context-dependent. For example, CPUE of the non-native brown trout *S. trutta* was positively associated with IWH in King Parrot Ck. but not in Shepherd Ck. Catch rates of brown trout were very low in Shepherds Ck., which probably reduced our ability to detect any possible effect, given that salmonids have been shown in other studies to respond to changes in coarse wood loadings (Sievers, Hale & Morrongiello, 2017). This context-dependence is also likely to be driven by differences in environmental conditions between sites. The importance of other habitat variables is discussed below, but these trends highlight the importance of considering system-specific attributes when planning instream rehabilitation actions.

Although the overall trend was for a positive effect of IWH, this response was not consistent across all species. One explanation of why blackfish responded less consistently (across systems) than Murray cod may relate to the life history and behaviour of the two species. Strong associations between river blackfish distribution and abundance and instream habitat density have been demonstrated at micro- and mesohabitat scales (Koehn et al., 1994; Koster & Crook, 2007; Howson et al., 2012). Furthermore, juveniles can respond more strongly to wood additions than adults can (Howson et al., 2012), consistent with the size effect observed. Landscape ecologists discuss the 'scale of effect', which describes the scale at which an ecological response (e.g. fish abundance) is most strongly related to landscape structure (e.g. IWH density) (Jackson & Fahrig, 2012; Jackson & Fahrig, 2015). The scale of effect is predicted to be positively correlated with traits such as home range size, dispersal ability, and body size (Miguet, Jackson, Jackson, Martin, & Fahrig, 2016), although empirical support for these relationships was mixed in a recent review of terrestrial species (Jackson & Fahrig, 2015). The more consistent response across systems observed for Murray cod rather than blackfish is consistent with this theory, although with the former having been recorded moving large distances to occupy sites subject to restored IWH (Lyon et al., 2019) whereas the latter are thought to have small home ranges (Koster & Crook, 2017). We would therefore expect blackfish to respond to habitat at smaller spatial scales, which has been shown, but to exhibit weaker associations at larger scales than Murray cod.

The relationship between fish CPUE and IWH density was generally found to be strongest when both of these variables were at lower levels. This is an important finding for considering likely responses to future IWH restoration actions. It suggests that restoring IWH is likely to lead to more pronounced changes in fish abundance in reaches that are more degraded, both in terms of historical IWH removal, and the population status of the native fish community. Other studies have found a correlation between fish responses and the amount of restored IWH. For example, coho salmon response was higher at restored sites in western Oregon and Washington streams where wood was deficient before restoration (Roni & Quinn 2001). This highlights the importance of understanding the initial conditions of both the IWH and fish population at sites to be able to predict likely responses.

Our model predictions between measures of fish abundance and IWH density also provide information to predict likely responses to habitat restoration actions or, conversely, the potential detrimental effects of historical desnagging (in addition to other system alterations such as river regulation and non-native species). For example, the model predicts on average a 4.07-fold increase (95%CI 2.03-8.15) in abundance of Murray cod following a change in IWH density from the present low levels observed in our study to the predicted natural levels in the region (from 0.001 – 0.0437m^2 m^{-3}; Kitchingman et al., 2016). These findings, when viewed in conjunction with the large-scale reductions in IWH loads across Victoria (Tonkin et al. 2016), provide further strong evidence that IWH loss is likely to have had major adverse impacts on the health of south-eastern Australian fish populations.

Knowing the scales at which different fish species respond most strongly to habitat will help determine the scale at which restoration efforts are likely to have the strongest impact traits (Hale et al., 2019). We did not directly compare the effects of scale, rather we compared the results that were focused at a scale that incorporated all of the functional river elements (mesohabitats) with previous work at meso- and microhabitat spatial scales. Also, a functional management scale, the Index of Stream Condition reach, was used as the basis to define a 'reach' based on the broad values and uses of rivers (see Ladson et al., 1999). In the future, it will be important to extend this work to consider different scales justified by the organisms of interest. The strongest evidence about the effects of scale on fish responses would come from a sampling design that incorporates a nested hierarchy of scales chosen to test *a priori* predictions about a selection of species with different expectations: i.e. some that are expected to respond at smaller scales compared with others expected to respond at larger scales (Hale et al., 2019).

Although the focus here was primarily on fish associations with IWH, other habitat variables are also important. If these variables also change following restoration created by scour following habitat additions, native fish responses may be enhanced. It is important also to consider the effects of the sampling design, as the negative relationships observed between several species and depth may indicate that it is more difficult for electrofishing operators to see and capture fish, especially small individuals (Lyon et al., 2014). Nevertheless, for waterways with most sites sampled at shallower depths (Wannon R., Hughes Ck., and Cudgewa Ck.), there was a positive association with depth. In Hughes Creek there were positive effects of depth on priority native fish species (mainly river blackfish and Macquarie perch) with modelling predicting a 350% increase in fish abundance within sub-reaches of the waterway when mean depth increases from 0.3 m to 0.9 m. Land-use practices, geomorphological processes and subsequent sedimentation events have severely reduced the amount of deep water refuges and structural habitat in this waterway. As such, work is under way to aid river blackfish and Macquarie perch through the creation of deep-water refuges by installing IWH and rock structures to constrict the channel and scour its bed (Erskine, 2015).

It is important to consider how applicable our results are to other systems. The results are likely to be directly transferrable to other systems in southern Australia with similar elevations and species compositions, which was the intention of the site selection process. It would be interesting, though, to extend this work into river systems within this region that differ with respect to other factors that might influence the nature of fish–habitat associations, such as those with barriers to movement and those with more non-native species. Restoration is often done in an *ad hoc*, site- and situation-specific manner (Hobbs & Norton, 1996), and this would allow testing of the generality, or context-dependency, of the relationships observed here to inform IWH restoration in other systems. It is also important to consider how applicable our results might be to other countries. Whereas there has been considerable work done examining fish responses to IWH restoration (Kail, Hering, Muhar, Gerhard, & Preis, et al. 2007; Whiteway et al. 2010, Roni et al. 2015; Donadi, Sandin, Tamario, & Degerman, 2019) the focus has been mainly on northern hemisphere species, especially salmonids. Extending the geographical focus of this work, as the present study does, will help a more general understanding of IWH restoration to be developed.

Streams were only sampled once but it is important also to consider factors that can affect the temporal trajectory of restoration. In particular, extreme hydrological events (i.e. droughts and floods) can potentially constrain or in some cases provide opportunities for restoration (Reich & Lake, 2015). It might be expected, for example, that flooding leads to a redistribution of wood that could alter the nature of fish–habitat associations (Stout et al., 2018). Alternatively, periods of drought could reduce the amount of available habitat. IWH might play a vital role in creating and maintaining refuges during drought conditions. Rivers exposed to IWH and riparian removal shift to a more homogenized bed profile, thus reducing the persistence, frequency and depth of pools (Wallace, Webster, & Meyer, 1995; Brooks, Brierley, & Millar, 2003). This study has provided a snapshot of fish–habitat associations, but it will be important to consider that these might vary through time.

5. CONCLUSIONS AND FUTURE DIRECTIONS

Setting goals and monitoring progress toward these is a critical element of any restoration programme (Palmer et al., 2005). This study provides a useful example of how quantitative data on the relationships between intended responses (more fish) and intended actions (IWH restoration) can help management agencies make more informed decisions about where and how to restore habitats. While IWH is often the focus of stream restoration (Roni et al., 2008), such actions can be limited by the availability of wood and the high costs associated with installation (Howson et al., 2012).

This study and others from the region that have quantified instream habitat conditions (Kitchingman et al., 2016; Tonkin et al., 2016) provide important information to set goals and quantitatively predict how fish might respond to IWH restoration in waterways across south-eastern Australia. It is critical though, that the relationships shown between fish and IWH here are considered as part of an overall approach to objective setting that includes other factors that are likely to have contributed to declines or affect responses to restoration

(Beechie et al., 2010), thus allowing an assessment of which targets are reasonable. This approach of applying multiple intervention types to achieve ecological outcomes is gaining momentum in south-eastern Australia. For example, Raymond et al. (2019) recently reported positive outcomes for native fish in a river reach subject to multiple restoration actions including IWH, riparian revegetation, removal of a weir hindering fish movement, fencing out livestock, and controlling riparian vegetation.

It is critical that IWH restoration is not undertaken in isolation, with other threats and constraints identified together with the potential influence of management actions. Understanding the interactions between IWH and other environmental variables is critical (Wohl et al. 2019). For example, a recent synthesis has shown that large wood benefits trout in Sweden but that this response is enhanced at locations with decreased stream shading (Donadi et al. 2019). Understanding these interactions can help guide when IWH restoration may be more effective when coupled with other management actions. For example, adding large wood in combination with boulders produced a stronger response by trout than boulders alone (Louhi, Vehanen, Mäki-Petäys, & Muotka, 2016).

Understanding the relationships between target taxa and habitat variables is an important initial step in restoration programmes (Bond & Lake, 2003), and can help guide expectations of the responses that are likely to be observed. More studies that examine relationships between fish and IWH across large spatial scales can therefore help predict expectations of the timing and shape (e.g. thresholds) of responses and inform stakeholder expectations, especially when coupled with information about the various ways that wood recruitment, transport and storage change over time (Wohl *et al.* 2019). Stream restoration often successfully changes hydrological and biogeochemical processes but biodiversity outcomes often do not occur (Palmer et al., 2014). We hope that IWH restoration efforts that are more informed about the underlying relationships between fish and IWH will help target situations where biodiversity outcomes are more likely to occur, or at least temper expectations for situations when restoration is planned at locations where more subtle responses are expected.

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Figure captions

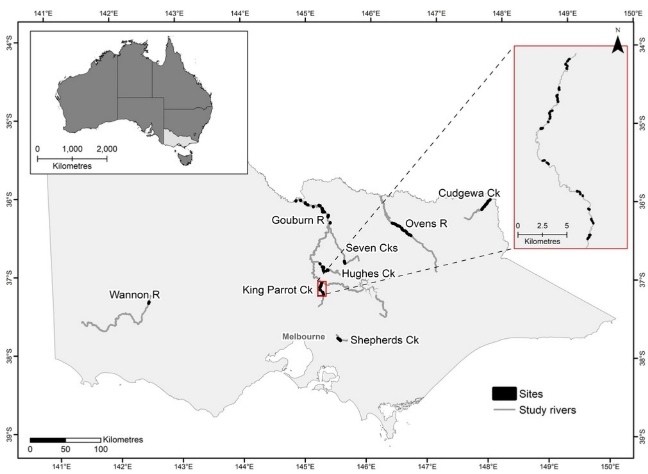
Figure 1: The location of the eight study waterways and associated fish survey sites across Victoria, Australia. Example of spatial distribution of sites within each waterway provided in the insert box.

Figure 2: Effect size estimates for IWH density (a) and vegetation overhang (b). Error bars are 95% credible intervals. Grey line indicates a slope of zero.

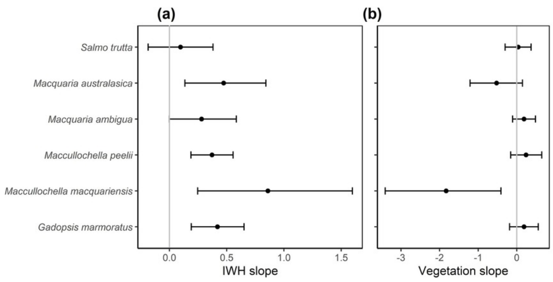
Figure 3: Effect of IWH density on catch rates per 100 m sampled. Model fits are shown for each species. Curves are model fit with 95% credible interval. Species curves only cover the actual range of IWH densities sampled for that species, as not all species are present in all river systems. Note - y-axis is log-scaled but capture rate numbers are on the raw scale (e.g. number of fish per 100m electrofished).

Figure 4: IWH effect sizes grouped by river. Estimates with 95% CI are from each species model and then grouped by river system. Grey line indicates a zero effect.

Figure 5: Effect size estimates for IWH density (a) and vegetation overhang (b) on average fish length. Error bars are 95% credible intervals. Grey line indicates a slope of zero.



AQC_3352_FIGURE 1.jpg



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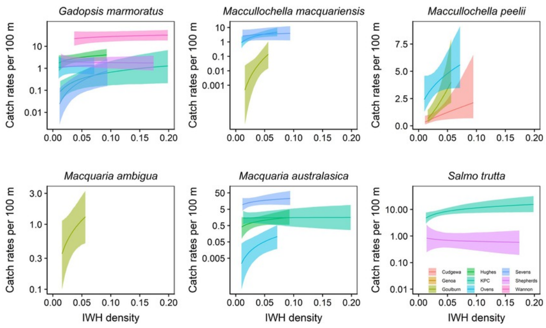

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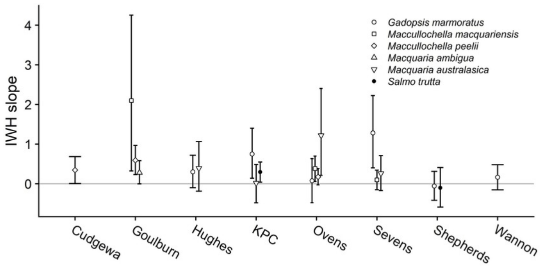

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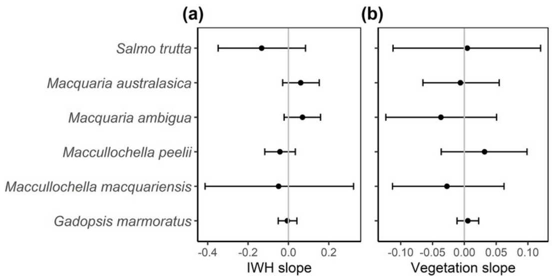

AQC_3352_FIGURE 5.jpg