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Article type : Original Article

Title Page

Using knowledge of behaviour and optic physiology to improve fish passage through culverts

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Improving fish passage through culverts

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/FAF.12446](https://doi.org/10.1111/FAF.12446)

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Abstract

Culverts reduce connectivity for aquatic animals by being both a hydraulic and physical barrier. However, altered light intensity may also be a behavioural barrier to fish movement, especially for diurnal species that have adapted to moving when it is light. We propose that knowledge of optical physiology and fish behaviour, two important mechanisms underpinning movement, can inform efforts to improve fish connectivity at culverts. We firstly review the sensory systems of fish with reference to visual sense and explore how this affects fish movement. We then highlight theoretical knowledge that can help us understand fish behaviour and the potential mismatch between the conditions under which fish have evolved and altered conditions within culverts. We describe potential knowledge gaps and directions for future research to improve our understanding of how culverts may affect fish movement. Finally, we explore the potential costs and ecological benefits of different mitigation options to identify those with the most promise for managing the light environment in culverts to facilitate movement. For researchers and managers exploring this subject, we suggest an approach that: (1) identifies light requirements for movement by different species, (2) tests movement under different light conditions, and (3) considers an integrative assessment method for testing fish behaviour around culverts. Understanding how optical physiology, fish behaviour, and culvert design influence fish movement can improve connectivity for a range of species.

Keywords: barrier, behavioural ecology, connectivity, culvert, light, movement

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65 **Introduction**

66 Connectivity is important for freshwater fishes (O'Connor, O'Mahony, &
67 O'Mahony, 2005; Pringle, 2003) as it allows them to complete all aspects of their life-
68 history linked with movement (Eiler, Nelson, & Bradshaw, 1992; McCormick, Hansen,
69 Quinn, & Saunders, 1998). However, habitat loss and fragmentation in streams and rivers
70 is occurring globally (Vorosmarty et al., 2010), meaning that connectivity is often
71 compromised. Disrupted movement is a major environmental problem that limits resource
72 access, restricts demographic exchange, and impedes gene flow (Cosgrove, McWhorter, &
73 Maron, 2018).

74 Large dams are the most dramatic examples of anthropogenic structures that
75 disrupt movement but smaller structures like culverts can also be barriers for fish (Warren
76 & Pardew, 1998). The global road network now totals >40 million lane-km (Dulac,
77 2013), which has resulted in culverts becoming some of the most widespread
78 anthropogenic riverine features (Goerig, Castro-Santos, & Bergeron, 2015). Culverts can
79 disrupt or prevent fish movement due to the presence of a drop at the outlet, high-water
80 velocities, or slope (MacPherson, Sullivan, Foote, & Stevens, 2012). Consequently, there
81 is a need to understand and manage their effects on migratory fish (Goerig et al., 2015).

82 Culverts can have a variety of designs (Figure 1), and will vary in terms of whether
83 and how fish can move through them (e.g. MacDonald & Davies, 2007). Understanding
84 fish swimming ability and hydraulic conditions in culverts is critical to predict passage.
85 Knowledge of the requirements for effective passage has improved substantially, with

agencies now developing fish passage guidelines incorporating contemporary designs (e.g. Franklin, Gee, Baker, & Bowie, 2018; O'Connor, Mallen-Cooper, & Stuart, 2015). The hydraulic principles designed into fishways are now being applied to culverts (e.g. MacDonald & Davies, 2007; Morrison, Hotchkiss, Stone, Thurman, & Horner-Devine, 2009).

The effects of culverts as both a physical and hydraulic barrier for fish are well understood. However, aspects of fish behaviour not related to swimming performance are also important. For example, there may be variability in the motivation of fish to enter and ascend culverts (Goerig & Castro-Santos, 2017). Changes to environmental conditions other than hydraulics may also be important, especially altered light regimes, which may mean culverts act as a behavioural barrier for fish (Kozarek, Hatch, & Mosey, 2017; Ono & Simenstad, 2014).

Human activities have dramatically altered light regimes in many environments, with a near ubiquitous increase in artificial light globally (Hölker, Wolter, Perkin, & Tockner, 2010). In the case of culverts, though, a lack rather than overabundance of light is a potential problem for some species (Figure 2). Yet while light intensity is likely to be an important factor in determining if fish move through instream structures (Bates, 2000; Boubée, Jowett, Nichols, & Williams, 1999; Cotterell, 1998), few studies have directly investigated fish responses to altered light environments in culverts (Box 1). The limited work that exists highlights that some fish avoid darkened culverts but this response is species-specific (M. Ali, Sakurai, & Collin, 1990; Amtstaetter, O'Connor, Borg, Stuart, & Moloney, 2017; Jones, Baumgartner, Zampatti, & Beyer, 2017). Considerable interspecific variation in responses to both light intensity and type have also been demonstrated more generally (Marchesan, Spoto, Verginella, & Ferrero, 2005; Patrick, Sheehan, & Sim, 1982). Understanding the sensory mechanisms underpinning this variability is important to identify which species are more likely to avoid moving into darkened culverts, and to help guide the development of management solutions.

We propose that knowledge of fish vision and behavioural ecology can help us understand how fish respond to altered light conditions as the basis for improving passage through culverts. Our aims are to: (1) review the sensory systems of fish to understand how altered light intensities may affect fish movement, (2) apply knowledge of fish

sensory systems to understand how culverts might impact movement of different fish species, (3) highlight how theories from behavioural ecology can help explain why the impacts of culverts on movement might vary, (4) identify key knowledge gaps and research opportunities and finally, (5) propose solutions to mitigate the impact of altered light environments in culverts on fish movement.

Sensory basis for understanding fish movement behaviour

Our aim in this section is to highlight how knowledge of fish vision, and sensory ecology more generally, can help understand variability in movement behaviour. This builds on detailed descriptions of the visual system of fish, and the links between vision and movement, that have been published previously (Douglas & Djamgoz, 1990; Lythgoe & Partridge, 1989).

Vision in fish is controlled by retinas containing rod and cone photoreceptors (M. A. Ali, 1959; Bowmaker et al., 2008). Rods contain the pigment rhodopsin which is sensitive at low light intensities for scotopic vision, while cones are responsible for photopic vision during high light intensities (Rodieck, 1973). Mesopic vision occurs during the transition between photopic and scotopic vision and uses a combination of rods and cones. McFarland et al. (1979) provided a detailed description of the changes that occur within the eye under different light conditions. When light intensity increases, the cones and melanin within the eye are extended towards the photoreceptor layer, with the rods effectively shaded by the melanin. Conversely, when light intensity decreases, the cones and melanin are withdrawn from the photoreceptor layer and the rods are extended and exposed to the dim light (McFarland, Ogden, & Lythgoe, 1979). Such changes effectively alter the neural circuitry from photopic to scotopic vision.

Fish that are most active during the night have evolved visual pigments and rod/cone ratios to maximise the amount of available light (S. P. Collin & Pottert, 2000; Landsberger et al., 2008). Conversely, fish that are most active during the day use cone-based vision, possibly including colour vision, to maximise the visible spectrum during daylight hours (Shaun P. Collin, 2009; Pignatelli, Champ, Marshall, & Vorobyev, 2009). Fish that are most active during the twilight period are likely to have a combination of rods and cones for mesopic vision (Stockman & Sharpe, 2006). Such evidence therefore,

suggests that vision in fish is linked with diel activity patterns (Lythgoe & Partridge, 1989).

While the structure of the eye (i.e. proportion of rods and cones) is an important component of when fish move, so too is the speed at which the eye can adapt to changes in light. Teleost fish have a rigid iris and a fixed pupil and therefore a period of retinal adaptation (retinomotor migration from photopic to scotopic vision) is required when faced with a light-dark transition such as a culvert. Much of the retinomotor migration duration work has focused on salmonids (M. A. Ali, 1959; M. A. Ali, Stevenson, & Press, 1961; Maksimovich & Gnyubkina, 2013; Wagner, 1980), with results indicating that it can take 1-2 hour for this adaptation to occur, and that adaptation from light adapted eyes to darkness takes longer compared with dark-adapted eyes are exposed to light.

Retinal pigments also vary in terms of the intensity of light required to initiate retinomotor migration (from photopic to scotopic vision), and this light intensity threshold may be equally as important as the duration of retinomotor migration (M. A. Ali, 1959). This threshold is likely particularly important when considering that predator-prey interactions and schooling maybe linked with visual ability (Azuma & Iwata, 1994; McMahon & Holanov, 1995; Petersen & Gadomski, 1994; Torisawa, Fukuda, Suzuki, & Takagi, 2011).

The circadian rhythm can also influence the transition between photopic to scotopic vision in fish (Sánchez-Vázquez & Tabata, 1998; Wang & Mangel, 1996). The circadian rhythm resets itself daily from environmental cues such as light-dark cycles. For fish, the process is thought to be controlled by the pineal organ (Ekstrzm & Meissl, 1997), which is a photosensory organ of the central nervous system that contains photosensory cells similar to the retina within the eye. The pineal organ provides photoperiod information to the brain via neural pathways (Ekstrzm & Meissl, 1997).

Studies into the spatial and temporal aspects of fish vision have also highlighted the optomotor response, or whole-body swimming, responses. It is taxonomically widespread (Nieman, Oppliger, McElwain, & Gray, 2018) but has been studied extensively especially with zebrafish (*Danio rerio*, Cyprinidae) (Orger & Baier, 2005). Optomotor tests are used to explore visual acuity by quantifying if fish can distinguish between different stimuli (often black and white), as the test subject will follow the moving stimuli while it can be

distinguished from the background. Changes in light environment can affect visual acuity and the optomotor response, such as when algal turbidity increases (Nieman et al., 2018).

The mechanosensory lateral line has also been studied in great length (Bleckmann, 2006; Mogdans & Kröther, 2001), and we know it is important in fish orientation (rheotaxis) (Montgomery, Baker, & Carton, 1997), sensing movement of prey and predators (Janssen & Corcoran, 1993), schooling behaviour (Partridge & Pitcher, 1980; Pitcher, Partridge, & Wardle, 1976), and for detecting changes in hydraulics (Baker & Montgomery, 1999). Both the lateral line and optomotor response are important for orientation within the environment.

Finally, it is important to consider sensory plasticity (Rauschecker, 1995) and how this may affect behaviour at culverts. Sensory plasticity occurs when an individual is deprived of one sense with a compensatory improvement in performance of another sense ie vision and chemoreception or hearing. Guppies raised in turbid waters for example, exhibited a stronger feeding response to chemical food cues compared with visual cues (Ben B. Chapman, Morrell, Tosh, & Krause, 2010). More specifically, developmental plasticity of spectral processing can result from a change during ontogeny, especially during the development of the visual cortex (Berardi, Pizzorusso, & Maffei, 2000; Hensch, 2005; Kröger, Knoblauch, & Wagner, 2003). Diurnally active species are likely to have developed visual sensory function relative to the local ambient conditions (allowing for relative variation in light intensity), and sensory plasticity plays an important role in adapting to changing conditions in the local environment (Ehlman, Sandkam, Breden, & Sih, 2015; Härer, Torres-Dowdall, & Meyer, 2017).

A conceptual model of fish movement behaviour at culverts and the role of vision

Based on the known link between vision and diel activity (Lythgoe & Partridge, 1989), there is likely to be variability in how different species are affected by darkened culverts based on when they are most active (Figure 3). In particular, the movement of those species adapted to photopic vision will be delayed when confronted with low light intensities from a culvert during the day (i.e. diurnal species, Figure 3). Species that require longer periods to adapt may be less likely to move when a rapid adaptation would be preferable to avoid predation or other negative impacts from delayed movement. A key

aspect will also be the degree to which light intensity within the culvert matches outside ambient light conditions. If high, fish may need a shorter adaptation period, hence avoiding the lengthy delay, and increase in predation risk. However, if the light level within the culvert is substantially lower than ambient conditions, fish eyes will need to adapt prior to moving through, therefore increasing the time delay and chance of predation.

While diurnal species may be most susceptible to changed light environments, some individuals that have coincidentally experienced light intensities similar to culverts during their early life-history may be less likely to be impacted. This would require a dedicated investigation to determine. It is also unlikely that diurnal species can rely on developmental plasticity (Smith-Gill, 1983) over short-term retinomotor adaptation. We acknowledge that lateral lines play a significant role in fish movement and orientation and may be utilized for negotiating darkened culverts. However, recent evidence suggests that vision also plays a major role in orientation and movement, indicating that multimodal senses are underpinning movement behaviour, particularly in complex flow environments (Liao 2007). Any retinal adjustment required before entering a darkened culvert may disrupt the rate of movement to the point where the culvert becomes a behavioural barrier. Such delays are especially likely in turbulent environments outside the culvert where neuromasts are saturated and functionality is compromised (Bassett, Carton, & Montgomery, 2006). We suggest therefore, that vision is likely to compliment or constrain movement through culverts, however additional research is required to fully understand its role in relation to other senses like the lateral line.

In contrast, nocturnal species adapted to scotopic vision are not generally active during the day, and so are not likely impacted by a darkened culvert. If a nocturnal species was disturbed however, they may seek refuge in a darkened culvert, although this is speculative. Crepuscular species most active during twilight conditions (Goerig et al., 2015; Peterson, Simmons, Cardoso, & Light, 2013) have mesopic vision and so contain visual pigments of both diurnal and nocturnal species. These species are more likely to be impacted by shady culverts compared with nocturnally active species, but less likely to be impacted than diurnal species.

We are unaware of any systems where information about the movement patterns of fish and their vision has been collected and applied to movement through culverts. However, predictions can be developed about which species might be most susceptible. In freshwater systems in southern Australia, river blackfish are generally nocturnal (Koster & Crook, 2007), and may be less likely to avoid darkened culverts than those that move during the day such as Australian smelt (*Retropinna semoni*, Retropinnidae), carp gudgeon (*Hypseleotris* spp., Eleotridae), unspecked hardyhead (*Craterocephalus stercusmuscarum fulvus*, Atherinidae), and bony herring (*Nematalosa erebi*, Clupeidae) (Jones et al., 2017; Mallen-Cooper, 1999). Ideally, such predictions will be tested using empirical data to understand variability in impacts on species with different movement behaviours.

Explaining the observed behaviour - theoretically

Concepts from the field of behavioural ecology can help us better understand the mechanisms that might underpin the variability in effects of culverts on fish movement (i.e. Figure 3). There has been considerable work to understand how animals respond behaviourally to changing environments (e.g. Candolin & Wong, 2012; Wong & Candolin, 2015). This research has highlighted that a key aspect is the degree to which present environmental conditions match the past environments under which the traits and behaviours of animals evolved (Andrew Sih, 2013; Andrew Sih, Ferrari, & Harris, 2011). Therefore, we need to know how different the light environment in culverts is to the conditions that fish have evolved under.

Signal detection theory (SDT) could help understand how fish respond to changes in light. SDT is a quantitative framework for analyzing cue-response relationships in the presence of uncertainty (Macmillan & Creelman, 2005) and can be used to help predict why only some animals respond adaptively to environmental change (Andrew Sih, 2013). SDT is often represented as a choice between two options, with each option having a distribution of cue strengths. Whether an animal can discriminate between these two distributions will determine their response; if they overlap, then discrimination and an appropriate response is likely. Animals will also have cue strength thresholds that must be exceeded before a response occurs (Andrew Sih, 2013). SDT is a useful way of visualizing how different fish might respond to culverts, based on the degree of match/mismatch in

the light environment in culverts and the environment they are adapted to, in combination with their response threshold (Figure 4).

Behavioural ecology provides the basis for assessing how animals evaluate and respond to different environmental cues and can be applied to thinking about how and why fish move through culverts. For example, fish can respond to cues from different sensory modalities (Ward & Mehner, 2010), and these cues could interact in different ways (Hale, Piggott, & Swearer, 2017). Experiments by Vowles et al. (2014) have shown that both light and hydrodynamic properties of water can be important cues for downstream migrating salmon. While multimodal cues might be important for migrating animals, this possibility has received little attention and has not applied to understand fish movement through barriers (Vowles, Anderson, Gessel, Williams, & Kemp, 2014). Nonetheless, the cues that trigger fish movement need to be understood to manage culverts. For example, some species may require not only light but another cue (e.g. odours from upstream conspecifics) to move. If so, it might be possible to harness knowledge of the sensory capabilities of fish to attract them upstream.

There is also increasing recognition in the field of behavioural ecology that not all individuals of the same species will behave in identical ways, and some exhibit 'behavioural syndromes' i.e. correlated suites of traits across different contexts (A. Sih, Bell, & Johnson, 2004; Andrew Sih, Cote, Evans, Fogarty, & Pruitt, 2012). This might mean that not all individuals of the same species are equally likely to move through culverts (Hale, Morrongiello, & Swearer, 2016). Some empirical work has provided evidence that this occurs, such as individual variability in trout motivation to enter and ascend culverts (Goerig & Castro-Santos, 2017). Bolder or more social fish may be more likely to explore and disperse (Cote, Clobert, Brodin, Fogarty, & Sih, 2010). Some individuals might also be neophobic (i.e. shown an aversion to novelty) and thus be less likely to move (Debeffe et al., 2014). Therefore, it is important to acknowledge that there may be individual variability in behaviour, especially in terms of responses to light. In turn, this may mean there is intra-specific variability in the degree to which altered light conditions affect movement. However, this possibility, and its potential population outcomes are not well understood.

Knowledge gaps and future research (vision, culverts and movement)

We have outlined how knowledge of fish vision and theories from behavioural ecology can help understand both inter- and intra-specific variability in the effects of culverts on fish movement behavior. However there have been limited attempts to apply this knowledge, and we highlight three important knowledge gaps that need to be addressed by future research.

What are the light requirements of different species?

We need to better understand the environmental conditions that different species require for movement. This information exists for some systems, such as salmonids in North America (e.g. P. N. Johnson, Bouchard, & Goetz, 2005; Kemp, Gessel, Sandford, & Williams, 2006). However, similar information is needed about how a wider range of species respond to light or shading (G. E. Johnson, Pearson, Southard, & Mueller, 2012). Experiments can be planned in an analogous fashion to studies examining the movement of terrestrial animals through road crossings (e.g. testing the influence of aperture diameter, substrate, length, light permeability (Woltz, Gibbs, & Ducey, 2008)). For culvert research and management, more field and laboratory based experimental work is especially needed to determine the light intensity thresholds and retinomotor adaptation periods for different species (e.g. Jones et al., 2017; Kozarek et al., 2017; Wagner, 1980), plus the influence of other factors such as culvert design versus fish behaviour (Figure 3). In the future, these data could inform the effect of changing light conditions within structures.

We have focused on mitigating the effects of changing light conditions to facilitate passage but equally we may be able to use differences in behaviour between native and exotic species to prevent or delay movement of the latter. Similar thinking has been applied in other situations such as fish traps in Australia that capture the exotic common carp (*Cyprinus carpio*, Cyprinidae), which exhibits jumping escape behaviour, while allowing native species to successfully pass upstream (Ivor G. Stuart & Conallin, 2018). A similar approach in relation to light could lead to selective exclusion of invasives (Rahel & McLaughlin, 2018).

While information about light requirements is needed, we also need to understand if these light thresholds translate into particular species avoiding culverts (sensu Jones et al.,

2017). A cost-effective way of conducting experiments to provide this information would be to use programmable light systems. This would allow the performance of different light regimes to be assessed, in terms of passage of both different fish species and size-classes. Sophisticated technologies now exist to track fish movement (e.g. tags, telemetry: Kessel et al., 2014). Statistical techniques like time-to-event, Markov, and poisson analysis (e.g. Castro-Santos & Haro, 2003; Goerig & Castro-Santos, 2017) can then be used to relate movement responses (e.g. attempt rate, migration delay, passage failure) to predictors like light intensity level and time of day and other covariates (e.g. discharge, fish length; Goerig & Castro-Santos, 2017). Combining these field- and statistical-techniques would be a powerful approach to examining the degree to which variability in movement can be related to light intensity, and potential interactions between light and other factors affecting fish movement.

Understanding the potential importance of phenotypic variability in behaviour

Studies showing variability in motivation (Goerig & Castro-Santos, 2017) are important for future experimental testing as they provide an opportunity to identify phenotypes that may be more likely to avoid culverts. Fish could be tagged, a subset of those that did and did not move recaptured, and then run through common laboratory-based behavioural assays (e.g. boldness and sociability trials). While more difficult, ideally these studies would be extended to examine if the fitness of fish (e.g. their ability to survive and breed) that migrate through culverts ultimately varies according to their phenotypes.

Considering the life histories of fish to understand the consequences of disrupted movement

The life histories of fish need to be considered to identify which phase of their life-cycle is most vulnerable to disrupted movement. Species that move obligately as part of their life cycle may be more likely to move through culverts regardless of light conditions. For instance, young-of-year diadromous Galaxiids (*Galaxias* spp. Galaxiidae) were recorded moving successfully through a 70-m long pipe culvert which was completely dark four metres from the entrance (Amtstaetter et al., 2017). Diadromous fish, though, are likely to differ in terms of the degree to which movements are obligate, with some

exhibiting ‘facultative diadromy’ (McDowall, 1988). For example, many populations of ‘amphidromous salmonids’ can contain some individuals who complete their life cycle completely in freshwater (B. B. Chapman et al., 2012). We thus might expect there to be considerable variability both among and within species in terms of their intrinsic motivation to migrate, with those with a strong innate response potentially being more likely to pass through culverts regardless of the ambient light environment. Activity changes associated with development (Ebner, Clear, Godschalx, & Beitzel, 2009) could also result in variable rates of susceptibility to darkened culverts.

By addressing these three knowledge gaps, we can start to develop a more holistic approach to managing fish passage through culverts. This should build on the historic focus on swimming ability and hydraulics, coupled with information about behaviour, physiology, and the effects of sensory cues such as light. Many of these factors have been discussed in the context of harnessing them to selectively prevent the movement of invasive fishes (Rahel & McLaughlin, 2018). Rahel and McLaughlin (2018) outline how biological traits like swimming ability, body morphology, sensory capability (e.g. responses to cues), behaviour, and phenology in terms of diel activity and seasonal migration patterns can fit within multi-dimensional niche space. Adapting a similar approach to thinking about culverts and adding in more information about behaviour and optical physiology (especially how long fish need to adapt to light, and the associated thresholds) could help further refine these expectations.

Potential mitigation options

Agencies worldwide have developed guidelines for improving waterway connectivity at road crossings such as culverts (King & Torre, 2007), often based on learnings from other fish passage facilities e.g. (Duguay, Lacey, & Castro-Santos, 2018). However, only a few acknowledge the potential effects of light on passage (I.G. Stuart, Berghuis, Long, & Mallen-Cooper, 2007), or suggest mitigation options (Boubee et al., 1999; Cotterell, 1998). In this section we discuss two important considerations for culvert management: (1) potential designs for new and existing structures, and (2) site selection and prioritization for retrofitting.

Potential options for designing new or retrofitting old structures

Fish passage programs typically identify a range of intervention options through a scoping study. In some instances, it may be possible that structures other than culverts. For example, low-lying bridges (Table 1), can fulfil similar engineering purposes and thus be built in place of culverts. Bridges generally provide increased light penetration and discharge capacity, and reduced water velocity and turbulence in comparison with culverts. Therefore, these structures may have less detrimental impacts on fish movement.

When building a culvert is the best option (e.g. in terms of costs; Table 1), knowing the light requirements of fish and the factors that underpin variability in movement can allow different designs to be considered. The basic shape and dimensions of culverts is a key consideration. For example, maximising the openness ration (i.e. cross-sectional area or diameter vs. length) can reduce the ‘tunnel effect’ and allow light to penetrate further (Ruediger, 2001). Using straight lines for longer culverts can help maximise the extension of light from the entrance and exit throughout the culvert as far as possible (Boubee et al., 1999). Box culverts should also be considered over pipe culverts as they provide a larger cross-sectional area for light penetration (in general) due to their fundamental shape (ie box versus cylinder). It may also be easier to design, construct and install baffles in box culverts to reduce turbulence where required, due to the absence of the radial curve in pipe culverts.

Culverts incorporating grates, holes or skylights on the upper portion of their structure will also allow additional light and rainfall to enter, and such, can help to reduce the impact of dark culverts and those with low openness ratios (Cotterell, 1998; Ruediger, 2001). Fishways throughout Australia use steel mesh (gridmesh) to cover the top of fishway cells to provide human access, but also to facilitate relatively natural light and rainfall conditions (I.G. Stuart et al., 2007). Also, Australian culvert and fishway crossings often incorporate light greates (Figure 5) following recommendations in Cotterell (1998) and research linking low light levels with lower fish passage rates (Jones et al., 2017; Mallen-Cooper, 1999).

New technological developments can be used both in the construction of new culverts, and to retrofit existing structures. For example, alternative materials such as recycled glass could be included during the culvert manufacturing process to increase light reflection and

transmission. Retrofitting culverts could be completed by coating them with reflective paint (ie road marking), or optical cable introduced to transmit light. Recent advances in light technology are especially promising and offer the potential for creating fit-for-purpose culverts. Programmable LED strip lighting is now relatively inexpensive and could be used to reproduce ambient light conditions, and be tailored to suit passage of individual species or size-classes with different light requirements.

Different designs and remediation actions will vary in terms of both effectiveness and cost (Table 1). Therefore, options must be trialled and their performance monitored. For example, gridmesh was used on a fishlock in Queensland, Australia, and was found to provide enough light (>386 lux) to facilitate passage of bony herring (I.G. Stuart et al., 2007), a species known to be light sensitive (Mallen-Cooper, 1999). Management agencies are likely to be more interested in alternatives that involve no or minimal addition cost. To facilitate the design, trialing, implementation and evaluation of different light solutions requires support from natural resource managers and policy makers, and possibly some innovative thinking within the culvert manufacturing sector and the agencies overseeing the design of new structures or retrofitting options. We have provided our best estimate of the likely relative cost and likelihood of the various mitigation measures being adopted and implemented (Table 1), but more evidence is needed to fully evaluate the costs and benefits of these options.

Site selection and prioritization for retrofitting

Central to mitigating the impact of culverts is a need to select sites that are a priority for restoration, both for engineering and ecological reasons. Prioritisation tools provide a quantitative and robust decision-making framework for handling multiple, potentially conflicting objectives (McManamay, Perkin, & Jager, 2019). For the road networks and culverts, potential considerations include function of the culverts (e.g. pedestrian access, vehicular access, ecological), length of stream to be rehabilitated, species migratory mode, other barriers, presence of exotic species and/or threatened species, and condition of the structure (e.g. poor, good, excellent) to name a few. This information can help managers to target those structures where greatest ecological benefits may be observed, while also considering competing budgetary requirement.

457

458 **Conclusion**

459 Large instream structures prevent fish movement and reduce connectivity over large
460 spatial scales. Yet the accumulating impact of smaller structures such as culverts may
461 have a similar effect. Researchers regularly document how poorly designed culverts
462 present a hydraulic and physical barrier but recent research suggests that their impacts
463 should be extended to include the possibility there are also behavioural barriers. We
464 suggest that diurnal species are more susceptible to darkened culverts than crepuscular or
465 nocturnal species due to their optical physiology. More sophisticated information about
466 the links between fish vision and light will help improve our understanding of the relative
467 sensitivity of different species. Incorporating insights from the extensive body of work on
468 wildlife crossing (e.g. susceptible species, what structural attributes that facilitate
469 movement and why) may help to accelerate learnings and positive outcomes, given the
470 conceptual similarities between crossings and culverts. By understanding the role of
471 optical physiology and behaviour around culverts, the effects of fragmentation on fish
472 movement may be better understood and effective mitigation solutions developed.

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474

475 **Acknowledgements**

476 We acknowledge funding from Melbourne Water and thank Dan Borg, Justin O'Connor,
477 Ivor Stuart, David Duncan, Ashley Sparrow and Andrew Boulton for commenting on the
478 manuscript. We also thank Ivor Stuart for photos of various culverts. We thank four
479 anonymous reviewers for comments that improved an earlier version of this manuscript.

480

481 **Data Availability Statement**

482 Data sharing is not applicable to this article as no new data were created or analysed in
483 this study.

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- Box 1: We conducted a systematic literature review to understand how fish movement through culverts is being studied. We searched the Web of Science database using the terms Fish* AND culvert*, which returned 260 records. We refined this list by including only quantitative studies (removing reviews and summaries of project-level outcomes) and those focused on fish movement through fishways (i.e. not changes in assemblage/genetics in upstream catchments), which left 91 studies. Three of these studies focused on the effects of light, with the remainder focusing on aspects of culvert design (e.g. slope, hydraulic conditions) and its influence on passage (e.g. passage success, swimming performance). Two of the three light studies examined the effects of strobe lights for reducing salmon entrainment in infrastructure (P. N. Johnson et al., 2005; P. N. Johnson, Goetz, & Ploskey, 2001), and the third experimentally showed how low light levels may inhibit movement of fish through culverts in southern Australia (Jones et al., 2017). We found no studies that mentioned fish vision or optic physiology. This review shows that the effects of the light environment on fish movements through culvert have been understudied.

790 **Table 1** Techniques used to improve light levels within artificial structures including culverts. Note. Potential for implementation and cost are based on the
 791 authors estimate –Low cost = \$AUD10K’s, Medium cost = \$AUD50K’s, High cost = \$AUD100K’s.

Method	Considerations	Cost	Benefit	Potential for Implementation
<i>Construction</i>				
Install grates/holes in structures	Planning/design required in advance	Low	Let light in at key locations, applicable to other instream structures	High - currently being implemented
Oversize culvert	Additional construction cost	Medium-High	Allows additional light in culvert	Medium
Align culvert in a straight line	May not be possible	Low-High	Allows light to transmit into structure	Low
Orientate culvert with sun	May not be possible, only temporally effective with transitioning sunlight	Low-High	Allows light to transmit into structure	Low
Install box or arch culvert instead of pipe culvert	Additional engineering/construction cost	Medium-High	Allows additional light in culvert	Medium – decision process hard to find
Provide shaded light at entrance of culvert	Will alter with time of day. Additional cost. Not always possible i.e large river and fishway. Outcome unclear	Low	Mitigates sharp light-dark transition point, allows retinal migration to begin, potentially reducing predation, applicable to other instream structures	Low
Install clear span bridge rather than culvert	Additional engineering/construction cost	High	Significantly more light than any culvert design, reduced hydraulic issues, reduces tunnel effect	Low
<i>Retrofit</i>				
Install artificial lights	Costly, maintenance requirements,	Low	Programmable, can target specific species, light intensities, or maybe	Medium, concept is

	effects unknown for most species		deter species, applicable to other instream structures	being implemented
Install solar reflector or fiber optical technology	Effectiveness unknown, may alter with angle of sun	Low	Parabolic mirror; Cats eyes are cheap, reliable, tested, applicable to other instream structures. Fiber optic cable can transmit light long distance	Medium
Use reflective construction materials	Materials yet to be identified, some pipe culverts are plastic, no precedent	Low-Medium	Can be readily incorporated into current design without concrete mould change, no maintenance required, applicable to other instream structures	Medium

Figure 1 Representative examples of box and pipe culverts commonly observed in south-eastern Australia. Note the darkened culvert and transition from light to darkness.

Figure 2 Changes in light conditions within a 12-m long round culvert (Victoria River, south-eastern Australia) across 24 hours of monitoring. Shown are light levels (a) outside the culvert, and (b) inside the culvert entrance, middle, and exit. Note the dramatically different y-axis scales. Figure re-drawn from data in Jones et al. (2017). Fish passage is not likely to occur for diurnal/photopic fish species through the culvert given the low light levels documented in graph B.

Figure 3. Conceptual diagram of how diurnal, crepuscular and nocturnal fish species are impacted by instream culverts. Diurnal fish species are likely to be particularly disadvantaged if abrupt changes in light conditions result in them congregating below structures, increasing both delays in movement and vulnerability to predation. Similarly, the same situation could occur above the culvert during downstream migration.

a). Day time - diurnal fish are actively trying to migrate upstream through the culvert but are reluctant to pass through because their eyes are adapted to daylight (photopic vision) and because of perceived threat of predation – few fish attempt passage or successfully pass; diurnal species are also prone to predation by predatory birds. Nocturnal fish remain inactive while crepuscular fish will opportunistically predate on prey if they are within close proximity.

b). Sunrise and sunset - diurnal fish movement increases (sunrise) or decreases (sunset). Predatory crepuscular fish are active while predatory bird activity increases (sunrise) or decreases (sunset). Nocturnal species movement decreases (sunrise) or increases (sunset).

c). Night time – diurnal fish and predatory birds are inactive. Nocturnal fish are active while crepuscular fish are also active.

Figure 4 Illustration of how signal detection theory can help understand the likelihood that fish avoid darkened culverts. In scenario 1, a fish species experiences a similar light regime when a culvert is constructed (grey line, “Culvert”) to the regime under which it has adapted (black line, “Historical”). In Scenario 2, a fish species experiences a culvert light regime that is

different to that under which it has evolved. The behavioural response of this species (i.e. does it avoid a culvert) will also be linked to its physiological response threshold. For example, a species with a low threshold (A) might be more likely to avoid a culvert than a species with a higher threshold (B) that occurs within the overlap between the distributions of “Historical” and “Culvert” light regimes. Figure adapted (Andrew Sih, 2013)

Figure 5. Gridmesh being used at a culvert and fishway crossing to allow light penetration onto the water surface below. Photos from south-eastern Australia.

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Title:

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Date:

2020-02-28

Citation:

Jones, M. J. & Hale, R. (2020). Using knowledge of behaviour and optic physiology to improve fish passage through culverts. FISH AND FISHERIES, 21 (3), pp.557-569. <https://doi.org/10.1111/faf.12446>.

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