# Darkness as a Behavioural Barrier to Fish Passage Through Long Culverts and Other Enclosed Crossing Structures

Lee F.G. Gutowsky, Tyana A. Rudolfsen

Fisheries and Oceans Canada
Ontario and Prairie Region
Freshwater Institute
501 University Crescent
Winnipeg, MB R3T 2N6

2026

Canadian Technical Report of
Fisheries and Aquatic Sciences 3818

Fisheries and Oceans Canada | Pêches et Océans Canada

Canada

**Canadian Technical Report of Fisheries and Aquatic Sciences**

Technical reports contain scientific and technical information that contributes to existing knowledge but which is not normally appropriate for primary literature. Technical reports are directed primarily toward a worldwide audience and have an international distribution. No restriction is placed on subject matter and the series reflects the broad interests and policies of Fisheries and Oceans Canada, namely, fisheries and aquatic sciences.

Technical reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in the data base *Aquatic Sciences and Fisheries Abstracts*.

Technical reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page.

Numbers 1-456 in this series were issued as Technical Reports of the Fisheries Research Board of Canada. Numbers 457-714 were issued as Department of the Environment, Fisheries and Marine Service, Research and Development Directorate Technical Reports. Numbers 715-924 were issued as Department of Fisheries and Environment, Fisheries and Marine Service Technical Reports. The current series name was changed with report number 925.

**Rapport technique canadien des sciences halieutiques et aquatiques**

Les rapports techniques contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui ne sont pas normalement appropriés pour la publication dans un journal scientifique. Les rapports techniques sont destinés essentiellement à un public international et ils sont distribués à cet échelon. II n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques de Pêches et Océans Canada, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports techniques peuvent être cités comme des publications à part entière. Le titre exact figure au-dessus du résumé de chaque rapport. Les rapports techniques sont résumés dans la base de données *Résumés des sciences aquatiques et halieutiques.*

Les rapports techniques sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre.

Les numéros 1 à 456 de cette série ont été publiés à titre de Rapports techniques de l'Office des recherches sur les pêcheries du Canada. Les numéros 457 à 714 sont parus à titre de Rapports techniques de la Direction générale de la recherche et du développement, Service des pêches et de la mer, ministère de l'Environnement. Les numéros 715 à 924 ont été publiés à titre de Rapports techniques du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 925.

Canadian Technical Report of
Fisheries and Aquatic Sciences 3818

2026

# Darkness as a Behavioural Barrier to Fish Passage Through Long Culverts and Other Enclosed Crossing Structures

by

Lee F.G. Gutowsky, Tyana A. Rudolfsen

Fisheries and Oceans Canada
Ontario and Prairie Region
Freshwater Institute
501 University Crescent
Winnipeg, MB R3T 2N6

© His Majesty the King in Right of Canada, as represented by the Minister of the Department of Fisheries and Oceans, 2026

This work is licensed under the Open Government Licence

Cat. No. Fs97-6/3818E-PDF ISBN 978-1-100-00973-5 ISSN 1488-5379

https://doi.org/10.60825/seek-zs55

Correct citation for this publication:

Gutowsky, L.F.G., Rudolfsen, T.A. 2026. Darkness as a Behavioural Barrier to Fish Passage Through Long Culverts and Other Enclosed Crossing Structures. Can. Tech. Rep. Fish. Aquat. Sci. 3818: viii + 55 p. https://doi.org/10.60825/seek-zs55

## TABLE OF CONTENTS

1. INTRODUCTION ..... 1
2. METHODS ..... 2
2.1 LITERATURE IDENTIFICATION ..... 2
2.2 SCREENING AND EVIDENCE CLASSIFICATION ..... 3
2.3 DATA EXTRACTION ..... 4
2.4 EVIDENCE SYNTHESIS ..... 4
3. CHARACTERISTICS OF THE EVIDENCE BASE ..... 5
4. IS DARKNESS A BEHAVIOURAL BARRIER TO FISH PASSAGE? ..... 10
4.1 EVIDENCE FROM CULVERTS AND PIPE SYSTEMS ..... 10
4.2 EVIDENCE FROM FISHWAYS AND EXPERIMENTAL ANALOGUES ..... 12
4.3 DARKNESS AS AN ABSOLUTE VERSUS PARTIAL BARRIER ..... 14
4.4 INTERACTION WITH HYDRAULIC AND STRUCTURAL CONDITIONS ..... 15
5. VARIATION AMONG SPECIES, GUILDS, LIFE STAGES, AND ENVIRONMENTAL CONDITIONS . 16
5.1 SPECIES AND ECOLOGICAL GUILD ..... 16
5.2 LIFE STAGE AND MIGRATION DIRECTION ..... 19
5.3 SEASON, DIEL PERIOD, AND AMBIENT LIGHT ..... 20
5.4 OTHER ENVIRONMENTAL MODIFIERS ..... 22
6. EFFECTIVENESS OF MITIGATION MEASURES ..... 23
6.1 ARTIFICIAL INTERIOR ILLUMINATION ..... 23
6.2 MAINTAINING NATURAL LIGHT ..... 25
6.3 GRADUAL TRANSITION ZONES ..... 26
6.4 PHYSICAL AND HYDRAULIC REMEDIATION ..... 27
6.5 SUMMARY OF MITIGATION EVIDENCE ..... 28
7. CONCEPTUAL MODEL OF DARKNESS-RELATED PASSAGE ..... 31
7.1 APPROACH ..... 31
7.2 ENTRY ..... 32
7.3 TRANSIT ..... 32
7.4 COMPLETION ..... 33
7.5 RETENTION AND UNSUCCESSFUL EXIT AFTER ENTRY ..... 33
7.6 FACTORS MODIFYING PASSAGE AT EACH STAGE ..... 34

7.7 INTEGRATED INTERPRETATION ..... 35
8. STRENGTHS AND LIMITATIONS OF THE EVIDENCE ..... 35
8.1 LIMITED DIRECT EVIDENCE FROM ROAD CULVERTS ..... 36
8.2 TAXONOMIC AND GEOGRAPHIC REPRESENTATION ..... 36
8.3 DIFFERENCES AMONG STUDY STRUCTURES ..... 37
8.4 HETEROGENEOUS LIGHT EXPOSURES ..... 37
8.5 LIMITED TRANSFERABILITY OF ILLUMINANCE THRESHOLDS ..... 38
8.6 VARIATION IN PASSAGE ENDPOINTS ..... 38
8.7 CONFOUNDING WITH PHYSICAL AND TEMPORAL CONDITIONS ..... 39
8.8 INCONSISTENT REPORTING OF ENVIRONMENTAL CONDITIONS ..... 39
8.9 UNRESOLVED HISTORICAL EVIDENCE ..... 40
8.10 OVERALL STRENGTH OF INFERENCE ..... 40
9. IMPLICATIONS FOR ASSESSMENT AND REGULATION ..... 42
9.1 INTERPRETING DARKNESS AS A POTENTIAL BEHAVIOURAL BARRIER ..... 42
9.2 CONFIRMING HYDRAULIC AND STRUCTURAL PASSABILITY ..... 43
9.3 CONSIDERING THE TARGET FISH ASSEMBLAGE ..... 43
9.4 EVALUATING LONG OR HIGHLY ENCLOSED CROSSINGS ..... 44
9.5 USE OF ARTIFICIAL LIGHTING ..... 45
9.6 MONITORING PASSAGE AND BEHAVIOURAL RESPONSES ..... 46
9.7 REGULATORY INTERPRETATION ..... 46
10. KNOWLEDGE GAPS AND RESEARCH PRIORITIES ..... 48
10.1 EVIDENCE GAPS ..... 48
10.2 MECHANISTIC GAPS ..... 49
10.3 MITIGATION GAPS ..... 50
10.4 MEASUREMENT AND REPORTING GAPS ..... 51
11. CONCLUSIONS ..... 51
ACKNOWLEDGEMENTS ..... 52
REFERENCES ..... 52

## LIST OF TABLES

Table 1: Characteristics of the 16 Core Empirical studies, including geographic region, structure type and dimensions, taxa and life stages, movement direction, lighting exposure, and principal behavioural or passage endpoints. ..... 7

Table 2: Evidence for mitigation measures intended to address darkness-related behavioural barriers to fish passage. ..... 29

Table 3: Confidence in principal synthesis conclusions. ..... 41

## ABSTRACT

Gutowsky, L.F.G., Rudolfsen, T.A. 2026. Darkness as a Behavioural Barrier to Fish Passage Through Long Culverts and Other Enclosed Crossing Structures. Can. Tech. Rep. Fish. Aquat. Sci. 3818: viii + 55 p. https://doi.org/10.60825/seek-zs55

Darkness within long culverts is frequently identified as a potential behavioural barrier to fish passage, but the empirical basis for regulatory decisions remains limited. We conducted a targeted evidence synthesis of 16 Core Empirical studies published from 1959 to 2026, supplemented by synthesis, guidance, and contextual literature, to evaluate whether darkness affects fish approach, entry, transit, completion, and exit or retention and whether mitigation is effective. Only two Core Empirical studies primarily examined operational road culverts; most evidence came from experimental pipes, fishways, and flumes. Lighting conditions clearly altered behaviour, but responses varied among species, life stages, movement directions, diel contexts, structure types, and passage endpoints. Fish successfully traversed completely or nearly dark structures, including an 82.3 m experimental pipe and a 70 m road culvert after hydraulic remediation, showing that darkness is not a universal absolute barrier. Conversely, low light or overhead cover reduced approach, entry, movement, or passage rate for several diurnal and visually oriented fishes. Artificial illumination improved some outcomes but was neutral or adverse for others, including nocturnal or negatively phototactic migrants, and could increase entry without retention. Hydraulic and structural conditions frequently interacted with or outweighed lighting effects. Evidence for natural-light measures and transition zones was limited, whereas hydraulic remediation consistently improved passage through structures that remained dark. The current evidence does not support a universal illuminance or culvert-length threshold. Assessment and mitigation should be species- and site-specific, distinguish successive passage stages, and evaluate lighting together with a primary focus on hydraulics, aperture, length, entrance conditions, and ambient diel light.

# RÉSUMÉ

Gutowsky, L.F.G., Rudolfsen, T.A. 2026. Darkness as a Behavioural Barrier to Fish Passage Through Long Culverts and Other Enclosed Crossing Structures. Can. Tech. Rep. Fish. Aquat. Sci. 3818: viii + 55 p. https://doi.org/10.60825/seek-zs55

L'obscurité dans les longs ponceaux est fréquemment identifiée comme un obstacle comportemental potentiel au passage des poissons, mais les données empiriques servant de base aux décisions réglementaires demeurent limitées. Nous avons réalisé une synthèse ciblée des données probantes issues de 16 études empiriques fondamentales publiées entre 1959 et 2026, complétée par des synthèses, des recommandations et des publications contextuelles, afin d'évaluer si l'obscurité affecte l'approche, l'entrée, le transit, la traversée et la sortie ou la rétention des poissons, et si les mesures d'atténuation sont efficaces. Seules deux études empiriques fondamentales portaient principalement sur des ponceaux routiers en exploitation ; la plupart des données provenaient de conduites expérimentales, de passes à poissons et de canaux. Les conditions d'éclairage ont clairement modifié le comportement, mais les réponses ont varié selon les espèces, les stades de vie, les directions de déplacement, les périodes nycthémérales, les types de structures et les points d'arrivée du passage. Des poissons ont traversé avec succès des structures totalement ou presque obscures, notamment une conduite expérimentale de 82,3 m et un ponceau routier de 70 m après des travaux de réhabilitation hydraulique, démontrant que l'obscurité n'est pas un obstacle absolu et universel. À l'inverse, une faible luminosité ou une couverture végétale ont réduit l'approche, l'entrée, le déplacement ou le taux de passage pour plusieurs espèces de poissons diurnes et à vision périphérique. L'éclairage artificiel a amélioré certains résultats, mais s'est avéré neutre ou nuisible pour d'autres, notamment pour les migrateurs nocturnes ou à phototactique négative, et pouvait augmenter le nombre d'entrées sans pour autant retenir les animaux. Les conditions hydrauliques et structurelles ont souvent interagi avec les effets de l'éclairage, voire les ont surpassés. Les preuves concernant les mesures d'éclairage naturel et les zones de transition étaient limitées, tandis que la restauration hydraulique a systématiquement amélioré le passage à travers les structures restées obscures. Les données actuelles ne permettent pas de définir un seuil universel d'éclairement ou de longueur de ponceau. L'évaluation et les mesures d'atténuation doivent être adaptées à l'espèce et au site, distinguer les différentes étapes de passage et évaluer l'éclairage conjointement avec l'hydraulique, l'ouverture, la longueur, les conditions d'entrée et la luminosité ambiante diurne.

## GLOSSARY

**Approach** - The stage during which a fish encounters and responds to the hydraulic, structural, and visual cues associated with a crossing upon reaching the entrance.

**Attraction Flow** - Hydraulic flow conditions intended to help fish locate and enter a passage structure.

**Artificial Illumination** - Artificially supplied light (floodlights, string lights, etc.) used within or near a passage structure to alter the light environment experienced by fish.

**Artificial Light at Night (ALAN)** - Artificial lighting introduced during periods that would otherwise be naturally dark.

**Behavioural Barrier** - A condition that influences a fish's willingness to approach, enter, persist within, or complete passage through a structure without necessarily exceeding its physical swimming capacity.

**Darkness** - Reduced or absent visible light within an enclosed crossing structure.

**Delay** - An increase in the time required for a fish to enter, transit, or complete passage relative to an alternative condition or treatment.

**Entry** - The transition from the exterior environment into an enclosed passage structure.

**Exit** - Departure from a structure after entry without successful passage completion, including return toward the entry location.

**Hydraulic Barrier** - A physical impediment to passage caused by hydraulic conditions such as excessive velocity, inadequate depth, turbulence, or outlet drops that exceed the swimming capabilities of a fish.

**Overhead Cover** - A treatment or structural condition that reduces light availability by covering a passage route.

**Passage Completion** - Successful movement from one end of a structure to the other, resulting in emergence beyond the crossing.

**Passage Rate** - The speed or frequency at which fish successfully move through a structure, often expressed relative to time.

**Retention** - Persistence within a structure following entry. Retention indicates that a fish remains in the structure rather than immediately exiting or passing.

**Retreat -** Movement away from a structure or passage route following approach.

**Route Rejection** - A behavioural response in which a fish approaches a passage route but does not proceed, instead retreating and/or switching routes.

**Transit -** Movement through the interior of a passage structure after entry.

# 1. INTRODUCTION

Road–stream crossings commonly rely on culverts, some of which extend for tens to hundreds of meters and create long, enclosed passageways (Slatick 1970; Hotchkiss and Frei 2007; Jones and Hale 2020). Even where hydraulic conditions are within the swimming capabilities of a fish, individuals may delay, retreat, or fail to enter or complete passage. Accordingly, darkness and reduced illumination are sometimes identified in reviews and design guidance as potential behavioural barriers. However, the empirical evidence supporting this concern remains limited, taxonomically narrow, and inconsistent (Hotchkiss and Frei 2007; Jones et al. 2017; Jones and Hale 2020; Keep et al. 2021).

Most assessments of fish passage through culverts focus on hydraulic barriers, which physically constrain passage by presenting conditions that exceed the swimming capabilities of a species or life stage. Because culverts may contract the natural channel cross-section, they can produce elevated water velocities, reduced depths, turbulence, or discontinuities at the outlet that impede passage (Hotchkiss and Frei 2007). Canadian guidance generally emphasizes maintaining stream-like hydraulic and geomorphic conditions or meeting species-specific hydraulic performance criteria (e.g., DFO 2007, 2015, 2016, 2022a, 2022b). Behavioural barriers, by contrast, do not necessarily exceed a fish's physical capacity but influence its willingness to approach, enter, persist within, or complete passage through a structure (Jones and Hale 2020). Behavioural and hydraulic barriers may also interact, such that separating their effects can be difficult in field settings (Kemp and Williams 2008, 2009; Vowles et al. 2014).

Fish experience naturally dynamic underwater light environments. Light availability varies over diel, lunar, and seasonal cycles and is further modified by cloud cover, riparian canopy, water depth, turbidity, surface conditions, and overhead structure. Human activities can alter these natural conditions through artificial light at night, vegetation removal, and the construction of enclosed crossing structures. Consequently, darkness is not a simple binary condition. Biological responses may depend on absolute illuminance, spectral composition, the contrast between exterior and interior conditions, the rate of transition between light environments, prior visual adaptation, and the sensory ecology of the species or life stage being considered (Jones and Hale 2020; Bassi et al. 2022). Light conditions can influence orientation, schooling, predator avoidance, foraging, activity rhythms, and migratory behaviour, and responses may differ substantially among diurnal, crepuscular, and nocturnal fishes (Marchesan et al. 2005; Reebs 2002; Bassi et al. 2022; Keep et al. 2021). For the purposes of this review, *culvert darkness* and *darkness* refer broadly to reduced or absent visible light within an enclosed crossing structure, while artificial illumination, overhead cover, and abrupt light-to-dark transitions are treated as related but distinct exposure types.

We conducted a targeted literature review to synthesize current understanding of darkness as a potential behavioural barrier to fish passage at culvert crossings. The specific objectives were to: (1) review and synthesize available scientific information

regarding darkness as a behavioural barrier to fish passage through culverts and other enclosed crossing structures; (2) evaluate how behavioural responses to darkness vary among fish species, ecological guilds, life stages, and environmental conditions, including season, diel period, and ambient light conditions; and (3) evaluate the effectiveness of mitigation measures intended to reduce behavioural barriers associated with darkness in culverts. The review also identifies important knowledge gaps, uncertainties, and considerations for regulatory application. Although the review focuses most directly on culverts, it also considers experimental pipes, tunnels, fishways, and laboratory or field channels where these studies provide mechanistic evidence applicable to enclosed road-crossing structures.

## 2. METHODS

### 2.1 LITERATURE IDENTIFICATION

The literature review was conducted using a targeted evidence-synthesis approach designed to identify studies directly relevant to behavioural barriers associated with darkness in culverts and other enclosed passage structures. The review was not intended to be a comprehensive systematic review of all fish-passage literature. Instead, searches were focused on evidence relevant to three questions: (1) whether darkness or reduced illumination affects fish movement, behaviour, or passage; (2) whether responses vary among species, life stages, ecological guilds, movement contexts, or environmental conditions; and (3) whether mitigation measures can reduce or eliminate behavioural barriers associated with darkness.

Nine seminal or “seed” papers was identified from prior knowledge of the subject area. These included primary experimental studies and a foundational synthesis paper that directly addressed fish responses to darkness, reduced illumination, overhead cover, or artificial lighting in passage-related settings.

The reference lists of the seed papers were then examined through backward citation searching. References were retained for further screening when they addressed fish responses to light or darkness, movement through culverts, pipes, tunnels, fishways, or other enclosed structures, sensory or visual ecology relevant to passage, or mitigation measures intended to alter lighting conditions. Forward citation searching was also conducted for key recent synthesis and experimental papers to identify newer studies that had built on this literature.

Additional keyword searches were conducted using Google and Google Scholar. An initial search used the terms *culvert darkness fish passage*. A broader closure search subsequently combined synonyms for passage structures, lighting conditions, and movement responses, including terms such as *culvert*, *pipe*, *tunnel*, *fishway*, *darkness*, *low light*, *illumination*, *overhead cover*, *fish passage*, *movement*, and *avoidance*. Screening of the broader Google search continued through the first 13 results pages, at which point additional results were judged to yield effectively no new directly relevant studies. This stopping point reflected diminishing relevance rather than a predefined

page limit. The first 13 pages of Google results from the broader search were screened. Targeted searches were also conducted for older government reports and grey literature repeatedly cited in reviews and guidance documents. Finally, the reference lists of newly identified studies were scanned to determine whether additional directly relevant empirical studies had been overlooked.

The search process was considered complete when the broader synonym search produced few new direct empirical studies, the highest-priority historical reports available through targeted searching had been retrieved, and the final reference-list scan of newly identified studies yielded no additional studies directly addressing light as a behavioural barrier at culverts or closely related enclosed passage structures.

### 2.2 SCREENING AND EVIDENCE CLASSIFICATION

Candidate sources were screened according to their relevance to the review objectives, empirical design, passage setting, behavioural endpoints, and treatment of light or darkness. Preference was given to studies that manipulated or measured lighting conditions, quantified fish movement or passage, evaluated enclosed or partially enclosed structures, compared multiple species or life stages, or tested mitigation measures.

Retained sources were assigned to one of five evidence classes:

1. Core Empirical evidence comprised independent empirical studies that directly evaluated darkness, reduced light, overhead cover, or artificial illumination in relation to fish movement or passage.
2. Core Synthesis/Seed sources comprised foundational reviews that directly framed the mechanisms, terminology, or conceptual basis of the review but did not provide independent experimental evidence.
3. Supporting Empirical evidence comprised empirical studies that informed interpretation of the core evidence but did not directly isolate the effect of light or darkness, or in which lighting was only an ancillary component of the study.
4. Context and Guidance sources comprised reviews, design guidance, annotated bibliographies, and technical reports used to describe historical practice, regulatory context, terminology, or proposed mitigation measures.
5. Secondary-only historical claims comprised findings reported in reviews, guidance, or memoranda for which the original primary source could not be retrieved and independently evaluated.

Only Core Empirical studies contributed directly to the principal evidence synthesis. Supporting Empirical studies were used where they informed interpretation of the core evidence, while secondary-only historical claims were documented separately and were not treated as independently verified evidence.

Studies focused exclusively on hydraulic performance, engineering design without behavioural evaluation, or unrelated aspects of fish ecology were excluded from the

main synthesis, although some were retained as contextual literature where they helped distinguish behavioural from physical barriers.

### 2.3 DATA EXTRACTION

For each retained empirical study, information was extracted into a structured evidence database, where fields were a reflection of the topics available in the literature. Extracted fields included:

- study setting and structure type;
- structure length, diameter, and other relevant dimensions;
- species, ecological group, and life stage;
- movement direction and migratory context;
- lighting treatment or exposure type;
- measured light intensity, where reported;
- environmental and hydraulic conditions;
- behavioural or passage endpoint;
- sample size and study design;
- quantitative results;
- mitigation measure evaluated;
- relevance to each review objective;
- evidence strength;
- principal limitations and uncertainties.

Lighting exposures were distinguished where possible among complete or near-complete darkness, low illuminance, overhead cover, abrupt light transitions, natural illumination, and artificial lighting. Passage outcomes were also separated into approach, entry, delay, rejection, transit, completion, and exit (i.e., passage failure) or retention because a lighting treatment could affect different stages of passage in different directions.

Passage endpoints were interpreted within a common framework. Approach describes movement toward the structure; entry is movement into it; transit is progression through its interior; and completion requires emergence beyond the opposite opening. Following entry, fish may also remain within the structure or leave through the entrance without completing passage. These outcomes were distinguished because lighting can affect them differently.

### 2.4 EVIDENCE SYNTHESIS

The empirical literature was highly heterogeneous in study setting, species, life stage, movement direction, lighting treatment, passage endpoint, and statistical reporting. Consequently, a single pooled effect estimate or conventional meta-analysis was not considered appropriate.

The evidence was instead synthesized using a combination of:

- descriptive counts of study characteristics;
- structured summaries of effect direction;
- within-study quantitative contrasts where comparable information was available;
- stratification by directness to culvert passage;
- stratification by species group, life stage, movement direction, lighting exposure, and behavioural endpoint;
- qualitative assessment of evidence strength and transferability.

Where possible, study-level results were expressed using measures such as differences in passage completion, ratios of passage or entry rates, ratios of median passage times, or reported hazard ratios. These measures were interpreted within studies rather than pooled across fundamentally different experimental designs and response variables. Greater weight was given to studies that directly manipulated light, used enclosed passage structures, measured multiple stages of passage, and provided clear treatment comparisons.

## 3. CHARACTERISTICS OF THE EVIDENCE BASE

Sixteen studies met the criteria for inclusion as Core Empirical evidence (Table 1). The studies were published between 1959 and 2026, with a median publication year of 2017; nine were published in 2017 or later. Study systems were geographically concentrated in North America, which accounted for eight studies, followed by Australia with four, Europe with three, and Asia with one.

Direct evidence from road culverts was limited. Only two studies had road culverts as their primary study setting. The remainder relied on experimental flumes or laboratory channels (eight studies), fishways (four studies), or experimental pipes and pipe fishways (two studies; Table 1). Thus, most of the evidence was derived from passage structures or experimental systems that reproduced particular characteristics of culverts—such as enclosure, overhead cover, light transitions, or restricted passage routes—rather than from controlled lighting experiments in operational road culverts. No independently reviewed tunnel study met the criteria for inclusion as Core Empirical evidence.

The evidence base was similarly concentrated taxonomically. Seven studies focused primarily on salmonids, while seven examined assemblages of small-bodied riverine fishes, including cypriniforms and Australian native fishes. One study examined galaxiids and one examined European Eel (*Anguilla anguilla*). Six studies focused on juveniles or young-of-year fish, four on adults or subadults, and six included mixed life stages or did not explicitly separate responses by life stage.

Eight studies evaluated upstream movement, six examined downstream movement, and two assessed voluntary or bidirectional movement. Movement direction was closely associated with taxonomic group and life stage: five of the six downstream studies examined juvenile salmonids, whereas the upstream studies included a broader range of taxa and life stages. This imbalance limits the extent to which findings from

downstream-migrating salmonid smolts can be generalized to upstream passage through culverts.

Twelve studies directly manipulated illumination or darkness, two manipulated overhead cover, and two measured behavioural or passage responses along naturally occurring light gradients. Most studies reported more than one response endpoint. Passage success or completion was evaluated in 15 studies, entry or route-selection responses in 13, transit time, passage rate, or delay in 11, and other behavioural responses—such as schooling, orientation, diel timing, or retention—in 12. The diversity of endpoints was important because darkness did not necessarily affect all stages of passage in the same direction.

Table 1: Characteristics of the 16 Core Empirical studies, including geographic region, structure type and dimensions, taxa and life stages, movement direction, lighting exposure, and principal behavioural or passage endpoints.

| Study | Region | Structure | Structure / length | Species / taxa | Life stage | Direction | Light treatment | Primary endpoint(s) |
|---|---|---|---|---|---|---|---|---|
| Jones et al. (2017) | Australia | Fishway | Vertical-slot fishway; first six cells used as a culvert analogue; length not reported | Australian Smelt, Unspecked Hardyhead, Bony Herring, Carp gudgeon, Flathead Gudgeon and Eastern Gambusia (invasive) | Mixed / not separated | Upstream | Daylight, artificial light, low light and darkness (0–4,550 lx) | Upstream movement counts; assemblage composition |
| Tarena et al. (2024) | Europe | Flume / laboratory channel | Hydraulic flume with a scaled deep side-notch weir; length not reported | European Gudgeon and Italian Riffle Dace | Adults / subadults | Upstream | Daylight, darkness and two artificial-light-at-night intensities (0–118 lx) | Passage success; passage time; repeated-trial effects |
| Kemp et al. (2005) | North America | Flume / laboratory channel | Covered and uncovered experimental channels; length not reported | Subyearling fall Chinook Salmon | Juveniles / young-of-year | Downstream | Covered versus uncovered route under otherwise illuminated conditions | Channel choice; route rejection; passage counts |
| Kemp et al. (2006) | North America | Flume / laboratory channel | Experimental flume with short-abrupt and long-gradual submerged weirs | Chinook Salmon, Steelhead and Sockeye Salmon smolts | Juveniles / young-of-year | Downstream | Alternating illuminated and dark trials | Passage/non-passage; route choice; residence time; schooling and orientation |
| Kemp & Williams (2008) | North America | Flume / laboratory channel | Control, corrugated and cobble/boulder experimental channels | Chinook Salmon smolts | Juveniles / young-of-year | Downstream | Light (~1,313 lx) versus darkness | Route selection; rejection after entry; passage; swimming and orientation |
| Kemp & Williams (2009) | North America | Flume / laboratory channel | Artificial channel with a submerged low-head weir | Juvenile Pacific Salmonids, primarily Chinook Salmon | Juveniles / young-of-year | Downstream | Visible light versus darkness with infrared observation | Approach and passage; pass/reject; schooling; station-holding and orientation |
| Vowles et al. (2014) | North America | Flume / laboratory channel | Experimental flume with an orifice weir producing contrasting velocity gradients | Juvenile Chinook Salmon | Juveniles / young-of-year | Downstream | Light (~95 lx) versus darkness with infrared observation | Avoidance; delay; passage; movement response to accelerating flow |

| Study | Region | Structure | Structure / length | Species / taxa | Life stage | Direction | Light treatment | Primary endpoint(s) |
|---|---|---|---|---|---|---|---|---|
| Vowles & Kemp (2021) | Europe | Flume / laboratory channel | Two-route open-channel choice flume with an 8 m test area | European Eel | Adults / subadults | Downstream | Dark control and low/high artificial light at night | Initial response; route switching/rejection; route selected; passage time |
| Kozarek et al. (2017) | North America | Culvert | Three culverts of 36.6, 47.5, and 61.0 m, supplemented by shaded laboratory passageways | Topeka Shiner and associated prairie-stream fishes | Mixed / not separated | Bidirectional / voluntary | Natural culvert light profiles and shaded versus unshaded laboratory passageways | Movement probability; mark–recapture passage; shade selection |
| Keep et al. (2021) | Australia | Flume / laboratory channel | 12 m hydraulic channel, supplemented by a field survey of culvert light | Fly-specked Hardyhead, Australian Smelt, juvenile Australian Bass and Silver Perch | Mixed / not separated | Bidirectional / voluntary | Sharp light-to-dark transition; 0–2,535 lx; threshold trials at 2.5–400 lx | Dark-zone entry; time allocation; threshold entry probability; rheotaxis |
| Amtstaetter et al. (2017) | Australia | Culvert | 70 m long, 1.5 m diameter road pipe culvert | Young-of-year Common, Spotted and Climbing Galaxias | Juveniles / young-of-year | Upstream | Measured decline from exterior daylight to complete darkness within approximately 4 m | Passage probability before and after hydraulic remediation |
| Tarena et al. (2025) | Europe | Fishway | Operating vertical-slot fishway with alternating covered and uncovered pools | Brook Barbel, European Bullhead and Italian Riffle Dace | Mixed / not separated | Upstream | Covered versus open-sky pools under natural day and night conditions | Entry; pool transitions; complete passage; passage rate; diel timing |
| Wang et al. (2025) | Asia | Fishway | 655 m experimental reach within a 2,597 m vertical-slot fishway; the monitored segment was experimentally darkened | Three Schizothorax species | Mixed / not separated | Upstream | Sequential near-dark and natural-light treatment periods | Entrance efficiency; pool passage; diel timing; transit speed |
| Kammanankada et al. (2026) | Australia | Pipe / pipe fishway | 225 mm pipe entrance apparatus installed at two low-head weirs | Six native species, dominated by Western Carp Gudgeon and Empire Gudgeon | Mixed / not separated | Upstream | Natural light versus dark pipe conditions, plus a limited artificial-light pilot | Entry proportion; time to entry; retention and exit |

| Study | Region | Structure | Structure / length | Species / taxa | Life stage | Direction | Light treatment | Primary endpoint(s) |
|---|---|---|---|---|---|---|---|---|
| Long (1959) | North America | Fishway | 29.3 m pool-and-overfall experimental fishway | Predominantly adult Steelhead and a small number of Chinook Salmon | Adults / subadults | Upstream | Near-total darkness versus bright artificial light | Entry timing and hesitation; complete passage; transit time |
| Slatick (1970) | North America | Pipe / pipe fishway | Experimental pipes 27.4–82.3 m long and 0.3–0.9 m diameter | Adult Chinook, Sockeye and Coho Salmon and steelhead | Adults / subadults | Upstream | Illuminated versus nonilluminated interiors and abrupt versus gradual light transitions | Entry; passage completion; passage time and rate |

Overall, the evidence base provided substantial experimental information on behavioural responses to light, darkness, and enclosure, but comparatively little controlled evidence from long road culverts. Interpretation therefore required consideration of both the strength of causal inference within each study and the directness with which its findings could be transferred to culvert crossings.

## 4. IS DARKNESS A BEHAVIOURAL BARRIER TO FISH PASSAGE?

The available evidence indicates that darkness can alter fish behaviour and passage, but does not support its characterization as a universal or consistently directional barrier. Across the Core Empirical studies, reduced light, darkness, or overhead cover was associated in some settings with avoidance, delayed entry, reduced movement, slower passage, or lower passage probability. In other studies, fish passed successfully through completely dark structures, showed no detectable response to lighting, or moved more readily under dark conditions. The interpretation also depended on the response endpoint: lighting conditions could have different effects on approach, entry, transit, completion, and retention within the same study. The evidence therefore supports darkness as a potential partial or context-dependent behavioural barrier, rather than an absolute barrier applying across species and crossing structures.

### 4.1 EVIDENCE FROM CULVERTS AND PIPE SYSTEMS

Direct studies of darkness in operational road culverts were scarce. The most applicable evidence was provided by two culvert studies (Kozarek et al. 2017; Amtstaetter et al. 2017), a long experimental pipe study (Slatick 1970), a pipe-fishway entrance experiment (Kammanankada et al. 2026), and one supporting culvert study in which lighting was an ancillary treatment (Gregory et al. 2004).

Kozarek et al. (2017) evaluated Topeka Shiner (*Miniellus topeka*) and associated prairie-stream fishes using field observations and mark–recapture at large box culverts in Minnesota, supplemented by shaded and unshaded laboratory passageways. Across three box culverts measuring 36.6, 47.5, and 61.0 m, field mark–recapture data indicated partial movement limitation in the two longer structures for some fish groups. Culvert length and midpoint illuminance were strongly confounded ($r = -0.94$), so the field study could not isolate lighting as the cause. In short laboratory channels, Topeka Shiner and Fathead Minnow (*Pimephales promelas*) did not show consistent avoidance of shaded treatments, although Topeka Shiner showed a slight endpoint preference for 70% shade. The combined results therefore make the independent effect of light indiscernible rather than demonstrating no field effect.

Amtstaetter et al. (2017) provided evidence from a 70 m-long, 1.5 m-diameter road culvert used by young-of-year Common Galaxias (*Galaxias maculatus*), Spotted Galaxias (*Galaxias truttaceus*), and Climbing Galaxias (*Galaxias brevipinnis*). Light declined from approximately 87,500 lx outside the culvert to 22.6 lx at 1 m, 0.5 lx at 2 m, and 0.3 lx at 3 m; visible light was undetectable through much of the culvert interior. Following the installation of internal hydraulic remediation, estimated passage

probability increased from 0.03 to 0.41. Young galaxias therefore traversed a long section of complete darkness when hydraulic conditions and resting opportunities were improved. Because darkness was not manipulated independently of the hydraulic retrofit, the study cannot determine whether low light imposed some residual delay or reduction in passage. It does, however, demonstrate that complete darkness did not constitute an absolute barrier for the species and life stages examined.

Slatick (1970) conducted the most extensive controlled experiment involving passage through long partially and fully flooded pipes. Adult Chinook *Salmon (Oncorhynchus tshawytscha)*, Sockeye Salmon (*Oncorhynchus nerka*), and Coho Salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) voluntarily entered pipes ranging from 27.4 to 82.3 m in length. The principal lighting comparisons used a 0.6 m-diameter, 82.3 m pipe containing two 180° turns. All four species passed through the pipe without internal illumination, establishing that darkness alone did not prevent passage through this enclosed structure. Illumination nevertheless altered passage time and completion in species- and run-specific ways. In the flooded pipe, median passage time was significantly shorter under illumination than in the nonilluminated treatment for steelhead, declining from 24.4 to 7.0 min, and for fall Chinook Salmon, declining from 9.9 to 5.5 min. Completion by steelhead also increased from 55% without illumination to 98% with illumination. Sockeye Salmon moved somewhat faster when the pipe was illuminated, but the difference was not significant and completion was nearly identical. Summer Chinook showed the opposite, although nonsignificant, response: median passage was faster without illumination, and a higher percentage completed passage in the dark treatment. Coho Salmon moved more rapidly under illumination, but completion was lower than under nonilluminated conditions.

Slatick (1970) also compared abrupt and gradual transitions between illuminated pools and an unilluminated pipe. Passage times were similar under the two conditions, and all tested summer Chinook Salmon, Sockeye Salmon, and steelhead completed passage. Thus, neither darkness nor an abrupt transition into darkness consistently impeded the adult salmonids examined. The experimental conditions with very high artificial-light levels, smooth and level experimental pipes, and use of adult salmonids limit direct transferability to contemporary road culverts, but the study provides strong causal evidence that the effect of illumination depends on species, seasonal run, and the endpoint measured.

Kammanankada et al. (2026) examined entry by wild, small-bodied fishes into a 0.225 m-diameter pipe-fishway apparatus installed at two low-head weirs. Natural light increased retained fish counts by approximately 44% and was the only significant predictor of faster entry, increasing the entry rate by a factor of approximately 1.9. This suggests that illumination can improve attraction to or willingness to enter a narrow pipe. However, entry was not equivalent to retention: limited artificial-light trials produced high entry but also exit rates of approximately 95–98%. The findings therefore

indicate that natural light influenced entry behaviour, while localized artificial lighting did not necessarily result in fish remaining within or proceeding through the pipe.

Gregory et al. (2004) provided weaker supporting evidence from an operational culvert. Artificial lights were used as one of four ancillary incentives during controlled releases of hatchery juvenile steelhead in a 30 m box culvert. The authors reported no apparent change in movement when the lights were left on. Light intensity was not measured, the treatment was sparsely replicated, and the incentive data were excluded from the statistical analyses. Consequently, the study should be interpreted as a weak null result rather than evidence that illumination has no effect. The study's primary findings concerned the substantially clearer influence of hydraulic conditions and baffle configurations on upstream movement.

Taken together, the most directly applicable studies show that fish can enter and traverse long, completely dark culverts and pipes. They also show that light can influence entry speed, transit time, passage completion, and retention. The direction and magnitude of these effects were not consistent across species or study systems.

### 4.2 EVIDENCE FROM FISHWAYS AND EXPERIMENTAL ANALOGUES

Fishway and flume experiments provided stronger control over lighting treatments than most culvert studies, but their structural relevance varied. These studies isolated behavioural responses to darkness, artificial illumination, or overhead cover while controlling hydraulic conditions, thereby providing strong evidence of causation. However, fishways and short experimental channels differ from road culverts in length, aperture, hydraulic complexity, attraction conditions, and the spatial progression from daylight into darkness.

Jones et al. (2017) manipulated lighting in the first six cells of a vertical-slot fishway, which were treated as an analogue for an enclosed culvert. Experimental illumination was informed by light measurements from a 12 m road culvert. More than 64,000 fish from six species were collected. Upstream movement by several fish species including Australian Smelt (*Retropinna semoni*), Unspecked Hardyhead (*Craterocephalus stercusmuscarum fulvus*), Bony Herring (*Nematalosa erebi*), Carp Gudgeons (*Hypseleotris spp*.), and the non-native Eastern Gambusia (*Gambusia holbrooki*) was substantially lower under low-light and dark treatments, whereas the number of fish moving upstream under artificial illumination was similar to that under natural daylight. The study provides strong experimental evidence that low light can reduce upstream movement by some small-bodied, visually oriented fishes, although the fishway setting and abrupt treatment boundaries differ from a long culvert.

Keep et al. (2021) similarly found strong avoidance of darkness by two diurnal, small-bodied Australian fishes. Australian Smelt (*Retropinna semoni*) and Fly-specked Hardyhead (*Craterocephalus stercusmuscarum*) spent approximately 86% and 97% of their time, respectively, in the illuminated half of an experimental channel. Entry into darkness increased with illuminance, with estimated response thresholds differing

between species. In contrast, juvenile Australian Bass (*Percalates novemaculeatus*) preferred the dark treatment, and Silver Perch (*Bidyanus bidyanus*) did not display a simple light preference. These contrasting results demonstrate that darkness may inhibit entry by some visually oriented species while being neutral or preferred by others.

Overhead cover also reduced movement in several studies. Approximately three-quarters of downstream-migrating juvenile Chinook Salmon avoided a covered channel in Kemp et al. (2005), with most approach resulting in retreat. In an operating vertical-slot fishway, Tarena et al. (2025) found that overhead cover reduced passage rates by approximately 4.8-fold for Brook Barbel (*Barbus caninus*) and 7.1-fold for Italian Riffle Dace (*Telestes muticellus*). The response of European Bullhead (*Cottus gobio*) was weaker and not statistically significant overall, although entry and transitions between pools were reduced. These studies suggest that enclosed or covered passageways can affect willingness to enter or a fish's movement rate. However, overhead cover is not equivalent to complete culvert darkness, as it incorporates visual enclosure and perceived predation risk..

The salmonid flume experiments conducted by Kemp et al. (2006) showed that light also modifies responses to hydraulic and structural cues. Kemp et al. (2006) observed species-specific responses to illuminated and dark conditions during downstream passage over hydraulic gradients. Kemp and Williams (2008) found that Chinook Salmon smolts moved more slowly in darkness and responded differently to corrugated and structurally complex channels depending on illumination. Kemp and Williams (2009) reported that juvenile salmonids formed schools and actively approached a submerged weir under light, whereas fish in darkness did not school and were less likely to approach, pass, or reject the structure. These findings indicate that darkness can reduce active exploration and movement, rather than simply causing fish to drift passively through a structure.

Other experiments showed that darkness can reduce behavioural avoidance and thereby accelerate passage. Vowles et al. (2014) found that juvenile Chinook Salmon were more likely to avoid an accelerating hydraulic gradient under light than in darkness, with avoidance occurring in 45% and 12% of observations, respectively. Fish exhibiting avoidance experienced considerably greater delay and travelled farther within the experimental channel before passing the hydraulic gradient. Darkness therefore reduced the fishes' visual response to an adverse hydraulic cue and, in this context, facilitated passage rather than impeded it.

Long (1959) documented a similar separation between entry and transit. Adult steelhead hesitated and entered a narrow fishway opening more slowly under near-total darkness, but once they entered, median transit through the 29.3 m fishway was significantly faster in darkness than under bright artificial light: 2.0 min compared with 8.5 min. This experiment illustrates why a study measuring entry alone could characterize darkness as adverse, whereas a study measuring transit after entry could reach the opposite conclusion.

Recent fishway experiments further demonstrated that darkness is not uniformly adverse. Wang et al. (2025) found that entrance and pool-passage efficiencies of three plateau *Schizothorax* spp. were similar or higher during experimentally darkened periods than under natural light, although sample sizes were small and treatment periods occurred sequentially. Darkness also shifted diel timing and altered transit speed differently among species. Tarena et al. (2024) found that artificial light at night reduced passage success and delayed European Gudgeon (*Gobio gobio*), but increased passage performance by Italian Riffle Dace under some conditions. Vowles and Kemp (2021) showed that European Eels rejected an artificially illuminated downstream route, demonstrating that adding light can itself create a behavioural barrier for nocturnal or negatively phototactic migrants.

Overall, experimental analogues provide clear evidence that lighting conditions can cause behavioural changes relevant to passage. Their results are less conclusive about how frequently those responses produce a barrier in operational culverts. Strong causal evidence of light-related avoidance or delay must therefore be interpreted alongside the lower structural directness of these experiments.

### 4.3 DARKNESS AS AN ABSOLUTE VERSUS PARTIAL BARRIER

The collective evidence does not support darkness as an absolute barrier that consistently prevents fish passage. Adult salmonids passed through nonilluminated pipes up to 82.3 m long in Slatick (1970), young Galaxias spp. traversed a 70 m road culvert with a completely dark interior in Amtstaetter et al. (2017), and fish moved through all three box culverts examined by Kozarek et al. (2017), although partial movement limitation in the two longer structures could not be attributed specifically to lighting because culvert length and midpoint illuminance were strongly confounded. Darkness also had neutral or positive effects in several fishway and flume studies.

Evidence for partial behavioural effects was stronger. These effects differed among successive stages of passage:

**Approach and entry.** Darkness or overhead cover reduced approach or entry by juvenile salmonids, several diurnal Australian fishes, European species including Brook Barbel and Italian Riffle Dace, and small-bodied fishes tested in a pipe-fishway entrance apparatus. Long (1959) observed hesitation at the dark entrance, while Kammanankada et al. (2026) found faster entry under natural light. Conversely, Kozarek et al. (2017) found no consistent avoidance of shaded laboratory passageways, and Slatick (1970) found no effect of abrupt versus gradual light transitions in the larger experimental pipe.

**Transit and delay.** Darkness slowed movement by Chinook Salmon smolts in Kemp and Williams (2008) and reduced active approaches in Kemp and Williams (2009). Cover reduced passage rate in Tarena et al. (2025). In contrast, adult steelhead traversed the fishway in the Long (1959) experiment more rapidly in darkness, and darkness reduced visually mediated avoidance and associated delay in Vowles et al.

(2014). Slatick (1970) found both faster and slower transit under illumination, depending on species and seasonal run.

**Passage completion.** Jones et al. (2017) found lower upstream movement under dark and low-light conditions, and Slatick (1970) found a large illumination-related increase in completion by steelhead. However, completion by fall Chinook Salmon and Sockeye Salmon was almost unchanged, while summer Chinook Salmon and Coho Salmon sometimes had higher completion without illumination. Hydraulic remediation enabled passage through the dark culvert in Amtstaetter et al. (2017).

**Exit and retention.** Few studies measured what occurred after entry. Kammanankada et al. (2026) demonstrated that localized artificial light could encourage entry while being followed by very high exit (i.e., failure) rates. This finding cautions against treating initial entry or detection within a structure as evidence of successful passage.

Darkness is therefore best understood as a factor that can alter the probability or timing of passage at one or more behavioural stages. A fish may hesitate but subsequently pass quickly, enter readily but subsequently leave through the entrance, or complete passage after a delay. Classifying a structure as either passable or impassable without identifying the passage stage and endpoint may conceal biologically important behavioural effects.

### 4.4 INTERACTION WITH HYDRAULIC AND STRUCTURAL CONDITIONS

Lighting conditions rarely operated independently of the physical properties of the passage structure. In several studies, hydraulic or structural variables produced effects as large as or larger than those associated with light.

The interaction was particularly evident in Amtstaetter et al. (2017). The culvert interior remained dark before and after remediation, but passage probability increased substantially after the installation of baffles and resting areas. This indicates that poor passage before remediation was primarily associated with hydraulic conditions rather than darkness alone. Gregory et al. (2004) likewise documented responses to baffle configurations in the primary analysis, whereas the ancillary lighting trials produced no apparent change in movement but were not analysed statistically.

Slatick (1970) directly tested pipe diameter, velocity, water depth, turns, entrance geometry, and illumination. Fish generally passed more readily through the 0.9 m pipe than the 0.3 m pipe. A tapered entrance cone greatly increased entry into the smaller pipe, particularly for Sockeye Salmon and steelhead, but provided little benefit at the 0.6 m entrance. Passage was delayed at the two 180° turns, and water depth affected passage time and completion. These results show that apparent hesitation at a dark entrance can reflect the combined effects of aperture, transition geometry, flow, and illumination rather than light alone.

Flume studies demonstrated comparable interactions between illumination and hydraulics. Kemp et al. (2006) found that responses to short and gradual velocity

gradients varied among salmonid species and light conditions. Kemp and Williams (2008) showed that structural complexity affected route selection and rejection under both light and dark conditions. Vowles et al. (2014) found that visual information increased avoidance of accelerating flow; removing visible cues reduced avoidance and delay. Thus, illumination can increase a fish's ability to detect and respond to hydraulic features, but the resulting behavioural response may either facilitate or inhibit passage.

Entrance attraction also interacted with lighting in Kammanankada et al. (2026). Natural illumination accelerated pipe entry, while a cone trap and attraction flow increased the number of fish entering or retained. No single treatment fully explained passage behaviour, and artificial illumination produced different effects on entry and exit. Similarly, overhead cover experiments combined changes in illuminance with enclosure, visual contrast, and perceived structural complexity, making it difficult to attribute responses exclusively to absolute light level.

Evidence regarding turbulence, turbidity, and spectral composition was comparatively limited. Most studies did not manipulate these variables factorially, and some historical experiments used artificial illumination far brighter than would normally be proposed for a culvert. Nonetheless, the consistent pattern across the evidence base is that darkness should not be assessed in isolation. Its effect depends on the dimensions and configuration of the crossing, hydraulic conditions, resting opportunities, attraction at the entrance, the availability of alternative routes, and the sensory and motivational context of the fish.

## 5. VARIATION AMONG SPECIES, GUILDS, LIFE STAGES, AND ENVIRONMENTAL CONDITIONS

Responses to darkness and illumination varied substantially among the fishes examined. The direction of response could not be predicted from taxonomy alone and was often associated with visual ecology, diel activity, movement direction, life stage, hydraulic conditions, and the particular stage of passage being measured. Ecological guilds provide a useful framework for organizing these differences, but the categories are neither mutually exclusive nor consistently defined across studies. For example, a species may be both benthic and nocturnally active, while salmonids may shift their use of visual cues among life stages and migratory contexts. The available evidence therefore supports guild- and context-specific hypotheses rather than general rules applicable to all members of a taxonomic or ecological group.

### 5.1 SPECIES AND ECOLOGICAL GUILD

The clearest evidence of darkness avoidance was obtained for small-bodied, diurnally active fishes. In laboratory choice experiments, Australian Smelt and Fly-specked Hardyhead strongly preferred illuminated habitat and made fewer entries into darkness at low illuminance. Entry increased progressively with light intensity, but the approximate illuminance associated with a given probability of entry differed between the two species, indicating that even fishes within the same broad ecological guild did not share

a common response threshold (Keep et al. 2021). Upstream movement by several small-bodied Australian native fishes also declined under low-light and dark treatments in the fishway experiment conducted by Jones et al. (2017), while artificial illumination restored movement toward that observed under daylight conditions. Together, these studies suggest that visually oriented, diurnally active fishes may be particularly susceptible to reduced illumination when passage requires voluntary entry into a darkened area.

Responses among nocturnal, crepuscular, or negatively phototactic fishes differed markedly. Juvenile Australian Bass strongly preferred the dark portion of the experimental channel used by Keep et al. (2021), whereas Silver Perch showed no simple preference and responded partly to flow direction. European Eel, a nocturnally active and negatively phototactic migrant, was more likely to reject a downstream route exposed to high artificial light at night and was less likely to select the illuminated route (Vowles and Kemp 2021). These findings demonstrate that illumination intended to alleviate darkness may itself inhibit passage by species adapted to move under low-light conditions. Supporting evidence from experimental streams similarly showed that Creek Chub (*Semotilus atromaculatus*) movement occurred predominantly during darkness, although that study did not include an enclosed passage structure or experimentally manipulate illumination (Kanno et al. 2023).

Benthic ecology alone was not a consistent predictor of response. European Gudgeon, a small-bodied benthic cypriniform, had lower passage success and experienced greater delay under high artificial light at night than under dark conditions (Tarena et al. 2024). European Bullhead, another benthic species with nocturnal tendencies, showed a weaker overall response to overhead cover than Brook Barbel and Italian Riffle Dace, although cover reduced some components of entry and movement between fishway pools (Tarena et al. 2025). Silver Perch also failed to exhibit a simple preference for either illuminated or dark habitat in Keep et al. (2021). Benthic fishes may rely less strongly on visual information than water-column species, but the reviewed evidence was too limited and variable to support a general conclusion that benthic species are unaffected by darkness.

Schooling and water-column fishes frequently displayed responses consistent with reliance on visual information. Australian Smelt and Fly-specked Hardyhead avoided dark habitat in Keep et al. (2021), while juvenile Pacific salmonids altered schooling, station-holding, orientation, approach, and passage behaviour between light and dark treatments (Kemp et al. 2006; Kemp and Williams 2008, 2009). Under illuminated conditions, salmonid smolts formed schools and actively explored the experimental channel. In darkness, schooling was reduced or absent, fish were more diffusely distributed, and fewer individuals approached or passed the experimental structure (Kemp and Williams 2009). These effects indicate that darkness can alter the social organization and active movement of visually oriented fishes even when it does not prevent passage completely.

Salmonids were the most frequently studied taxonomic group, but their responses were not uniform. Juvenile downstream migrants often avoided overhead cover or showed reduced active movement in darkness (Kemp et al. 2005; Kemp and Williams 2008, 2009). However, darkness also reduced their ability to detect and respond to accelerating flow, thereby decreasing avoidance and associated passage delay in some circumstances (Vowles et al. 2014). Adult upstream migrants showed similarly variable responses. Long (1959) observed greater hesitation before entry into a dark fishway, but substantially faster transit once fish entered. Slatick (1970) found that adult Chinook Salmon, Sockeye Salmon, Coho Salmon, and steelhead all passed through nonilluminated pipes, while the benefits of artificial illumination varied among species and seasonal runs. Steelhead showed the clearest improvement in passage time and completion under illumination; fall Chinook Salmon moved faster when the pipe was illuminated, whereas summer Chinook Salmon exhibited a nonsignificant response in the opposite direction. Consequently, even within salmonids, the effects of lighting differed between juveniles and adults, upstream and downstream migrants, species, and seasonal runs.

Small-bodied cypriniform and leuciscid fishes were also well represented, particularly in recent European and Asian studies. European Gudgeon and Italian Riffle Dace responded differently to artificial light at night under the same experimental conditions: high artificial illumination reduced and delayed European Gudgeon passage but improved some measures of Italian Riffle Dace passage relative to darkness (Tarena et al. 2024). Overhead cover subsequently reduced passage rates of Italian Riffle Dace and Brook Barbel in an operating fishway, while the effect on European Bullhead was less pronounced (Tarena et al. 2025). In contrast, laboratory trials by Kozarek et al. (2017) found no consistent avoidance of shaded passageways by Topeka Shiner or Fathead Minnow, although their field observations could not isolate the influence of lighting from culvert length and other structural conditions. Wang et al. (2025) observed neutral or positive passage responses to experimental darkness among three *Schizothorax* species. The cypriniform evidence therefore spans avoidance, neutrality, and apparent facilitation by darkness.

Evidence for anguillids was limited to European Eel. The avoidance of artificial light by downstream-moving eels was consistent with their nocturnal and negatively phototactic ecology, but the experiment addressed artificial light at night rather than entry into a dark culvert (Vowles and Kemp 2021). Its principal relevance is that adding illumination cannot be assumed to improve passage for all migratory fishes.

Galaxiids provided an important counterexample to the assumption that small-bodied fishes cannot traverse long, dark structures. Young-of-year Common, Spotted, and Climbing Galaxias passed through a 70 m culvert whose interior reached complete darkness within a few metres of the entrance after hydraulic conditions were improved (Amtstaetter et al. 2017). Related studies showed that ramps, baffles, and reductions in velocity improved passage by galaxiids, although they did not directly evaluate light

(MacDonald and Davies 2007; Franklin and Bartels 2012). These findings suggest that darkness was not the primary constraint for the galaxiids examined and that their capacity to traverse a dark structure depended more strongly on hydraulic passability and resting opportunities.

Overall, broad ecological traits were informative but not determinative. Diurnal and schooling fishes most consistently avoided darkness, while nocturnal or negatively phototactic species were more likely to avoid artificial illumination. However, responses also varied within these categories, and neither benthic habit, small body size, nor taxonomic membership reliably predicted whether darkness would inhibit passage.

### 5.2 LIFE STAGE AND MIGRATION DIRECTION

Life stage and movement direction were strongly confounded with taxonomy in the available literature. Most downstream studies examined juvenile salmonids, whereas adult salmonids, galaxiids, and several small-bodied riverine fishes were studied primarily during upstream movement. Consequently, differences attributed to life stage or migratory direction may also reflect differences among species, experimental structures, and motivational states. Few studies compared life stages of the same species under equivalent light and hydraulic conditions.

Adult upstream-migrating salmonids demonstrated that darkness does not necessarily prevent motivated fish from entering and traversing enclosed structures. Fish tested by Long (1959) reported passage by 82 adult Steelhead and one Chinook Salmon during dark trials, compared with 100 Steelhead and three Chinook Salmon during illuminated trials. These counts describe the fish tested under each condition rather than differences in passage success. Fish entered more slowly and were observed to hesitate more at the narrow entrance gate in darkness, but traversed the fishway significantly faster after entering. Adult salmon and steelhead also passed through the nonilluminated pipes tested by Slatick (1970), including an 82.3 m pipe with two 180° turns. Illumination altered passage time and completion, particularly for steelhead, but the magnitude and direction of response differed among species and Chinook Salmon seasonal runs. Strong migration motivation and adult swimming capacity may have helped these fishes persist through enclosed structures, although neither study directly compared adults with juveniles.

Juvenile upstream migrants showed more variable responses. Young galaxiids traversed a long, completely dark culvert after hydraulic remediation (Amtstaetter et al. 2017), while small-bodied Australian fishes had lower upstream movement under low-light and dark fishway treatments (Jones et al. 2017). Natural illumination also accelerated entry by small-bodied fishes into a narrow pipe fishway in Kammanankada et al. (2026), and overhead cover reduced entry or passage rates for several small-bodied European species in Tarena et al. (2025). These studies indicate that darkness may be more consequential at the decision to enter or continue through a structure than as a physical impediment once passage has begun.

Downstream-migrating salmonid smolts were the subject of a comparatively cohesive body of experimental work. These fishes frequently avoided covered routes, altered schooling and orientation in darkness, and approached or passed experimental structures less often when visual information was unavailable (Kemp et al. 2005, 2006; Kemp and Williams 2008, 2009). However, the absence of visual cues could also reduce active avoidance of hydraulic gradients and shorten the delays associated with rejection behaviour (Vowles et al. 2014). Darkness therefore did not have a consistently adverse effect on downstream passage. Rather, it reduced visually mediated decision-making, which could either suppress active migration or reduce avoidance of a passage route.

The available anguillid evidence concerned downstream-moving European Eels approaching a choice between illuminated and dark routes. High artificial light at night increased rejection of the illuminated route, consistent with the nocturnal behaviour of migrating eels (Vowles and Kemp 2021). This response should not be generalized to adult fishes moving upstream into dark culverts, but it is directly relevant to the risk of using artificial lighting where downstream anguillid migration occurs.

Studies of voluntary or bidirectional movement provide information about preference and willingness to enter dark habitat in the absence of strongly standardized migratory motivation. Keep et al. (2021) found pronounced species-specific light preferences during voluntary movement within an experimental channel. Kozarek et al. (2017), in contrast, found no consistent avoidance of shaded laboratory passageways. Their field observations indicated some movement limitation in the two longer culverts, but the strong confounding between culvert length and illuminance prevented that limitation from being attributed specifically to interior lighting. Together, these findings suggest that resident movement responses may be highly species-specific and may not predict behaviour during directed seasonal migrations.

Movement direction must therefore be considered when interpreting evidence for a behavioural barrier. Avoidance of an illuminated route by a nocturnal downstream migrant is not evidence that darkness will facilitate upstream entry. Similarly, reduced schooling by downstream smolts in darkness does not necessarily predict passage by resident or upstream-moving small-bodied fishes. The strongest conclusions are those limited to the species, life stage, and migratory context actually studied.

### 5.3 SEASON, DIEL PERIOD, AND AMBIENT LIGHT

Fish responses to culvert lighting occur within naturally varying diel and seasonal light environments. However, relatively few studies separated the effects of experimental illumination from time of day, season, or prevailing ambient conditions.

Studies that incorporated natural day and night periods demonstrated species-specific diel patterns. In the operating fishway studied by Tarena et al. (2025), the effects of overhead cover varied among species and passage stages, while movement also differed between day and night. Wang et al. (2025) found that experimental darkness

altered the diel distribution of upstream passage by plateau fishes, in some cases shifting movement toward daytime hours. A supporting fishway study found that barbel passage occurred significantly more often at night than during daylight, although illumination was not experimentally manipulated (Eggers et al. 2025). Similarly, most Creek Chub movement in experimental streams occurred during darkness, but temperature and individual condition also influenced movement (Kanno et al. 2023). These studies show that diel activity can modify the response to an enclosed or illuminated structure, but natural day–night comparisons alone cannot identify light as the causal mechanism.

Artificial light at night represents a different exposure from the absence of light inside a daytime culvert. This distinction means that artificial illumination should not be assumed to offset the behavioural effects of darkness. Light introduced during a naturally dark period can disrupt diel behaviour or repel nocturnal migrants. Tarena et al. (2024) found that artificial night lighting reduced passage and increased delay for European Gudgeon, but Italian Riffle Dace passed more rapidly under the same conditions. Vowles and Kemp (2021) found that high artificial light increased route rejection by European Eel. These findings caution against treating artificial illumination as simply the inverse of darkness. Responses are species- and context-dependent: illumination that facilitates movement under some conditions may inhibit passage or alter behaviour under others.

Seasonal effects were rarely tested directly. Slatick (1970) observed different illumination responses among spring, summer, and fall salmon runs, including contrasting results for summer and fall Chinook Salmon. Seasonal run, population, water conditions, and the timing of the experiments were not fully separable, however, and the results cannot establish that season itself caused the differences. More generally, species availability and migration timing determined when individual taxa could be tested in several field and historical studies. Apparent species differences may therefore partly include seasonal differences in motivation, physiological condition, or environmental conditions.

Ambient light at the entrance and the contrast between exterior and interior conditions may be as important as the absolute light level within a structure. Long (1959) observed hesitation as adult salmonids entered a narrow dark opening from an illuminated approach area. Keep et al. (2021) found strong responses to a sharp transition between illuminated and completely dark channel sections. Natural illumination increased and accelerated entry into the pipe apparatus used by Kammanankada et al. (2026). In contrast, Slatick (1970) found no difference between abrupt and gradual transitions from illuminated pools into a nonilluminated 0.9 m pipe. The effect of contrast may therefore depend on entrance dimensions, species, motivation, and the availability of hydraulic or visual cues.

The time required for visual acclimation or adaptation was seldom measured. Repeated passage trials improved performance by European Gudgeon and Italian Riffle Dace in

Tarena et al. (2024), but the design could not distinguish visual adaptation from learning or increasing familiarity with the experimental structure. Most experiments exposed fish to comparatively abrupt treatment changes and monitored responses over short periods. The evidence base therefore provides little information on whether fish approaching a culvert gradually adapt to declining light or whether repeated encounters reduce initial hesitation.

### 5.4 OTHER ENVIRONMENTAL MODIFIERS

Environmental variables other than light were reported inconsistently and were rarely manipulated in combination with illumination. As a result, their role as modifiers of behavioural responses could generally be inferred only from individual studies.

Water clarity is likely to influence both the amount of light penetrating a culvert and the distance over which fish can detect structural or hydraulic cues. Several laboratory experiments were conducted in clear water, including the threshold trials of Keep et al. (2021), whereas turbidity was not consistently reported in the broader evidence base. Long (1959) indicated that water clarity and turbidity were similar between experimental days, but did not manipulate them. No reviewed Core Empirical study provided a controlled test of the interaction between turbidity and illumination in a culvert. Quantitative light thresholds derived under clear laboratory conditions should therefore not be assumed to apply under turbid field conditions.

Temperature was commonly reported as a background condition but was seldom evaluated as an interaction with light. The salmonid flume experiments were conducted over defined but relatively narrow temperature ranges, and the Long (1959) study occurred under stable temperatures during each comparison. Supporting evidence from Kanno et al. (2023) showed that temperature and individual body condition influenced Creek Chub movement under natural light–dark cycles. This suggests that physiological state and temperature may modify willingness or capacity to move, but the present literature cannot separate those effects from the influence of lighting in passage structures.

Flow and hydraulic conditions were among the strongest modifiers identified. Salmonid responses to illumination changed with velocity gradients, discharge, and structural complexity in the Kemp and Vowles experiments (Kemp et al. 2006; Kemp and Williams 2008, 2009; Vowles et al. 2014). Slatick (1970) found that pipe velocity, diameter, water depth, turns, and entrance geometry all affected passage, sometimes more strongly than illumination. Passage by young galaxiids through a completely dark culvert increased substantially after velocities were reduced and resting opportunities were provided (Amtstaetter et al. 2017). Attraction flow also increased fish entry or retention in the pipe-fishway experiment of Kammanankada et al. (2026). These findings indicate that the behavioural effect of darkness depends partly on what fish encounter hydraulically after approaching or entering the structure.

Water depth was examined most explicitly by Slatick (1970). Fall Chinook Salmon, Coho Salmon, and steelhead sometimes moved faster or completed passage more often when pipes were partly filled rather than flooded. Because changes in water depth also altered available air space, hydraulic conditions, and potentially the distribution of light, the mechanisms could not be attributed to any single variable. Nonetheless, the results demonstrate that lighting responses observed in a flooded pipe may not transfer directly to a partially filled culvert.

Visual contrast and entrance geometry also interacted. The narrow 0.3 m pipe tested by Slatick (1970) was difficult for fish to enter until a tapered transition cone was installed, whereas the same treatment provided little benefit at the larger 0.6 m pipe. Long (1959) similarly attributed some hesitation to the narrow dark fishway entrance. These findings suggest that apparent avoidance of darkness may sometimes reflect a combined response to a small opening, abrupt enclosure, flow transition, and reduced visual information.

Collectively, environmental modifiers were insufficiently standardized to support generalized quantitative relationships. The available evidence nevertheless indicates that darkness is experienced in combination with flow, depth, aperture, visual contrast, temperature, water clarity, and prior exposure. Species- or laboratory-specific illuminance thresholds should therefore be interpreted as hypotheses for application and field testing rather than as broadly transferable passage criteria.

# 6. EFFECTIVENESS OF MITIGATION MEASURES

Evidence for mitigation of darkness-related behavioural barriers was limited and highly context dependent. Most studies evaluated lighting as an experimental treatment rather than as a permanent mitigation measure installed in an operational culvert. Furthermore, the studies differed in species, life stage, movement direction, structure type, light intensity, and the passage endpoint measured. Consequently, the evidence does not support a single mitigation measure that can be applied reliably across culverts and fish communities.

Artificial illumination improved passage for some fishes but was neutral or detrimental for others. Measures that maintained natural light or reduced overhead cover were generally beneficial to several diurnal and schooling species, although the evidence was derived largely from experimental channels, fishways, and pipe entrances rather than full-length culverts. Gradual light-transition zones remain conceptually plausible but have received little direct testing. By contrast, there was consistent evidence that addressing hydraulic and structural constraints can improve passage through structures that remain completely dark.

## 6.1 ARTIFICIAL INTERIOR ILLUMINATION

Artificial interior lighting produced the most variable results among the mitigation measures considered. In the vertical-slot fishway experiment of Jones et al. (2017), upstream movement by several small-bodied fishes was substantially lower under low-

light and dark treatments, whereas the number of fish moving upstream under artificial illumination was broadly comparable to that under daylight conditions. This study provides direct experimental evidence that artificial lighting can reduce a light-related behavioural limitation for some diurnally active fishes.

Slatick (1970) also found benefits of internal illumination, but the response varied among adult salmonid species and seasonal runs. In an 82.3 m experimental pipe, illumination significantly reduced median passage time for steelhead and fall Chinook Salmon. Completion by steelhead increased from 55% in the nonilluminated pipe to 98% under illumination. Sockeye salmon also moved somewhat faster under illumination, but completion was nearly identical between treatments. Summer Chinook Salmon showed a nonsignificant response in the opposite direction, with faster transit and higher completion in the nonilluminated pipe. Coho Salmon moved faster when the pipe was illuminated, but a lower percentage completed passage. These results indicate that illumination may improve one component of passage, such as transit speed, without increasing overall completion.

The lighting conditions used in historical experiments also limit their applicability to present-day culvert mitigation. Slatick (1970) used 75 W flood lamps that produced approximately 3,455 lx, at the bottom of an empty pipe. Long (1959) compared near-total darkness with artificial illumination of approximately 3,229–10,764 lx at the water surface. In the latter study, adult steelhead entered more readily under illumination but traversed the fishway substantially more slowly after entry. These light intensities were much greater than those likely to be proposed for most culvert retrofits and may have elicited responses that would not occur under lower or more spatially diffuse illumination.

Other studies found little or no apparent benefit of artificial lighting. Gregory et al. (2004) reported no apparent change in hatchery juvenile steelhead movement when lights were used as an ancillary incentive in a 30 m box culvert used for baffle trials. However, lighting was not quantified, was sparsely replicated, and was not included in the statistical analysis, making this a weak null result. In the pipe-entry experiment of Kammanankada et al. (2026), limited artificial-light treatments produced relatively high entry but were followed by exit rates of approximately 95–98%. Artificial illumination therefore did not ensure that fish remained within or proceeded through the pipe.

Artificial light can also inhibit passage. European Eel rejected an artificially illuminated downstream route, particularly under the higher artificial-light treatment, consistent with the species' nocturnal and negatively phototactic behaviour (Vowles and Kemp 2021). Tarena et al. (2024) found that high artificial light at night reduced passage success and increased delay by European Gudgeon, whereas Italian Riffle Dace passed at higher rates under artificial light than under darkness. These studies demonstrate that lighting intended to mitigate darkness for one species may create a behavioural deterrent for another.

Natural and artificial light should therefore not be treated as ecologically equivalent. Artificial lighting may differ from natural illumination in intensity, spectrum, direction, spatial distribution, timing, and contrast with surrounding conditions. It can also be introduced during periods that would otherwise be naturally dark. The available evidence supports artificial illumination as a potentially useful, species- and site-specific intervention, but not as a universal remedy for dark culverts. Where artificial lighting is considered, it should be evaluated using controlled trials that measure entry, passage time, completion, and exit or retention rather than entry alone.

### 6.2 MAINTAINING NATURAL LIGHT

Maintaining natural illumination may avoid some of the potential disadvantages associated with artificial lighting. One passive approach is to incorporate overhead grates, grated access covers, light wells, roof openings, or skylights into a long enclosed crossing. These features can introduce daylight at intervals, shorten the continuously dark portion of the passage route, and more closely retain the diel and spectral variation of natural light than continuous artificial illumination. Jones and Hale (2020) identified grates, holes, and skylights as potential design features for increasing natural illumination, while Keep et al. (2021) suggested that relatively small additions of light could remove a behavioural obstacle for some diurnally active fishes. In New Zealand, project designers for the Christchurch Southern Motorway Stage 2 and Main South Road Four Laning contemplated light wells and resting areas at approximately 40–60 m intervals along long, flat piped water-race sections (New Zealand Transport Agency 2013). Earlier New Zealand guidance also recommended straight alignments for long culverts so that daylight could penetrate along the barrel (Boubée et al. 1999).

However, these examples establish design feasibility and precedent rather than biological efficacy. No Core Empirical study reviewed here directly compared fish passage through otherwise similar culverts with and without overhead grates, skylights, or light wells. Keep et al. (2021) tested fish responses to low-light conditions in an experimental channel rather than evaluating a skylight or culvert retrofit, and the New Zealand motorway documents presented light wells as a proposed design measure rather than a monitored passage treatment. The current New Zealand Fish Passage Guidelines similarly conclude that direct evidence concerning the effects of light on passage remains limited and that implications for upstream passage by juvenile New Zealand fishes are ambiguous (Franklin et al. 2024). Overhead grates and light wells should therefore be characterized as plausible passive daylighting measures whose effectiveness remains unquantified, rather than as proven fish-passage mitigation.

The strongest empirical support comes from studies of natural light and overhead cover. Kammanankada et al. (2026) found that natural illumination increased retained fish counts by approximately 44% and nearly doubled the rate of entry into a narrow pipe-fishway entrance. Jones et al. (2017) found substantially greater upstream movement under daylight than under low-light or dark fishway treatments. Keep et al. (2021)

similarly documented strong preferences for illuminated habitat among Australian Smelt and Fly-specked Hardyhead.

Experiments involving overhead cover also suggest that retaining open-sky conditions can benefit some fishes. Approximately three-quarters of downstream-migrating juvenile Chinook Salmon avoided the covered route examined by Kemp et al. (2005). Tarena et al. (2025) found that overhead cover reduced passage rates by approximately 4.8-fold for Brook Barbel and 7.1-fold for Italian Riffle Dace in an operating fishway. The response of European Bullhead was weaker, illustrating that reducing cover would not provide the same benefit to all species.

Larger apertures may improve both light penetration and the physical transition into an enclosed structure. Slatick (1970) found that adult salmonids passed much more readily through a 0.9 m pipe than through a 0.3 m pipe. However, the study could not distinguish whether this response resulted from greater illumination, increased physical space, improved flow conditions, reduced confinement, or a combination of factors. Similarly, the addition of a tapered entrance cone substantially improved entry into the 0.3 m pipe without changing interior illumination. Aperture and entrance design should therefore be viewed as structural measures with potential secondary benefits for natural lighting rather than as proven darkness-specific mitigation.

The evidence for shortening structures and straightening alignments was also largely conceptual or guidance based. Slatick (1970) showed that 180° turns delayed passage, but fish nevertheless traversed the nonilluminated 82.3 m pipe. No Core Empirical study established a structure length, alignment, or spacing of daylight openings that reliably prevented a darkness-related behavioural response. Passive maintenance of natural light is therefore a defensible precautionary design principle, particularly for diurnal or schooling fishes, but its effectiveness cannot yet be quantified across crossing designs or fish assemblages.

### 6.3 GRADUAL TRANSITION ZONES

Gradual transition zones are intended to reduce abrupt changes between bright exterior conditions and a dark culvert interior. Potential measures include shading the approach, progressively reducing illumination near the entrance, using a series of lower-intensity fixtures, creating an acclimation area, or modifying entrance geometry to provide a less abrupt transition into enclosure.

Several observations suggest that entrance contrast could influence fish behaviour. Long (1959) observed that adult salmonids hesitated more and entered more slowly when the experimental fishway was dark. Keep et al. (2021) found strong avoidance by two diurnal species at a sharp transition between illuminated and completely dark channel sections. Natural light also accelerated pipe entry in Kammanankada et al. (2026). However, these studies did not isolate whether the response resulted from absolute darkness, visual contrast, entrance aperture, perceived enclosure, or other entrance conditions.

Slatick (1970) provided the most direct test of transition-zone mitigation. Adult summer Chinook Salmon, Sockeye Salmon, and steelhead were tested with abrupt and gradual transitions between illuminated pools and a nonilluminated 0.9 m pipe. Median passage times were similar under the two conditions, and all fish completed passage. The results provide no evidence that gradual light transitions improved passage for the adult salmonids and pipe dimensions examined.

The absence of an effect in Slatick (1970) does not establish that transition zones are ineffective for smaller, more strongly diurnal, or less motivated fishes. The tested pipe had a relatively large diameter, and the fish were adult upstream migrants with strong migratory motivation. Nevertheless, the available evidence is insufficient to recommend entrance shading, progressive lighting, or acclimation zones as a general requirement. These measures remain plausible options for site-specific experimentation where pronounced entrance hesitation has been observed.

### 6.4 PHYSICAL AND HYDRAULIC REMEDIATION

Physical and hydraulic remediation does not directly increase light availability, but it may be the most effective way to restore passage through a dark culvert where darkness co-occurs with excessive velocity, insufficient depth, poor entrance conditions, or a lack of resting opportunities.

Amtstaetter et al. (2017) provides the clearest example. The interior of the 70 m road culvert reached complete darkness within approximately 4 m of the entrance and remained dark following remediation. Nevertheless, the estimated passage probability of young galaxiids increased from 0.03 before remediation to 0.41 after the installation of internal baffles and resting areas. Fish therefore traversed a long section of complete darkness once the hydraulic challenge was reduced. This result indicates that darkness was not an absolute barrier and that hydraulic conditions were a more immediate constraint.

Supporting studies reached similar conclusions. MacDonald and Davies (2007) found that spoiler baffles increased passage success by Common Galaxias and Spotted Galaxias, with the most complex treatment producing approximately 80% passage success compared with 13.5% in untreated controls. Franklin and Bartels (2012) reported increased upstream species richness and fish density following the installation of a ramp and baffles in a 73.8 m culvert, although passage efficiency remained limited for some species. Neither study evaluated lighting directly, but both demonstrate that weak-swimming fishes can pass through enclosed structures when velocities, outlet conditions, and resting opportunities are improved.

In a 30 m box culvert in Oregon, Gregory et al. (2004) documented responses of hatchery juvenile steelhead to baffle configurations, whereas ancillary artificial-light trials produced no apparent change in movement but were not analysed statistically. Similarly, Slatick (1970) showed that pipe diameter, entrance geometry, water velocity, depth, and turns affected passage. A tapered entrance cone improved entry into the smallest pipe,

larger pipes were used more readily, and partly filled pipes sometimes produced faster passage and higher completion than flooded pipes.

Attraction flow and entrance design also affected entry in Kammanankada et al. (2026). A cone trap substantially increased retained counts, and attraction flow increased entry or retention independently of the lighting treatment. These findings reinforce that a fish must first locate and enter a crossing before interior light conditions can influence transit.

The evidence therefore supports a sequential approach to mitigation. Hydraulic and structural passability should first be confirmed or restored by addressing velocity, depth, turbulence, outlet conditions, aperture, resting opportunities, entrance geometry, and attraction flow. Darkness-specific mitigation should then be considered where behavioural delay or avoidance remains after these factors have been addressed.

### 6.5 SUMMARY OF MITIGATION EVIDENCE

Table 2 summarizes the evidence for each candidate mitigation measure, including the principal studies, species or context, observed response, direction of evidence, and confidence rating.

Table 2: Evidence for mitigation measures intended to address darkness-related behavioural barriers to fish passage.

| Mitigation | Principal studies | Species or context | Observed response | Evidence direction | Confidence |
|---|---|---|---|---|---|
| Artificial interior illumination | Jones et al. 2017; Long 1959; Slatick 1970; Gregory et al. 2004; Tarena et al. 2024; Vowles and Kemp 2021; Kammanankada et al. 2026 | Small-bodied riverine fishes, adult salmonids, juvenile trout, European Eel, European cypriniforms, pipe-entering fishes | Improved movement, transit, or completion for some species; neutral, slower, deterrent, or associated with high exit for others | Mixed and strongly species- and context-dependent | **Moderate–High that responses are context dependent; Low for universal effectiveness** |
| Maintaining natural illumination or open-sky conditions | Jones et al. 2017; Kemp et al. 2005; Keep et al. 2021; Tarena et al. 2025; Kammanankada et al. 2026 | Diurnal and schooling fishes; juvenile salmonids; small-bodied upstream migrants | Greater entry or movement under natural light; reduced use or passage under overhead cover for several species | Generally beneficial for visually oriented species, but not universal | **Medium** |
| Larger aperture and improved entrance openness | Slatick 1970; Kammanankada et al. 2026 | Adult salmonids and small-bodied pipe-entering fishes | Larger pipe or improved entrance geometry increased entry and passage; lighting contribution could not be isolated | Positive for passage, uncertain as a darkness-specific measure | **Medium for structural benefit; Low for light-specific attribution** |
| Shorter, straighter structures or daylight openings | Slatick 1970; Jones and Hale 2020; guidance sources | Long or highly enclosed culverts | Turns delayed passage; direct tests of shortening structures or adding daylight openings were absent | Conceptually favourable but empirically unresolved | **Low** |

| | | | | | |
|---|---|---|---|---|---|
| Gradual light transitions, entrance shading, or acclimation zones | Long 1959; Slatick 1970; Keep et al. 2021; guidance sources | Bright exterior-to-dark interior transitions | Entrance hesitation observed in some settings; abrupt versus gradual transitions did not affect passage in Slatick's adult salmonids | Plausible but not consistently supported | **Low** |
| Baffles, resting areas, and velocity reduction | MacDonald and Davies 2007; Franklin and Bartels 2012; Amtstaetter et al. 2017; Gregory et al. 2004 | Galaxiids, juvenile salmonids, and other weak-swimming fishes | Passage improved through structures that remained dark after hydraulic remediation | Consistently positive for hydraulic passability | **High for hydraulic benefit; not a darkness-specific treatment** |
| Improved depth and water-surface conditions | Slatick 1970 | Adult salmonids in flooded and partly filled pipes | Partly filled conditions sometimes improved transit and completion | Potentially positive, but species- and structure-specific | **Medium–Low** |
| Improved entrance geometry and attraction flow | Slatick 1970; Kammanankada et al. 2026 | Adult salmonids and small-bodied pipe-entering fishes | Tapered entrance, trapping configuration, and attraction flow increased entry or retention | Positive for attraction and entry | **Medium–High for entry; uncertain for complete passage** |

Overall, the evidence indicates that mitigation should be selected according to the target species, life stage, movement direction, and passage stage affected. Artificial lighting may be effective where a diurnal species avoids or delays entry into darkness, but it may be ineffective or detrimental for nocturnal fishes and may improve entry without improving completion. Maintaining natural illumination is generally preferable where it can be incorporated passively into the crossing design, although its benefits have not been quantified across the full range of culvert types. Where hydraulic or structural constraints coexist with darkness, those constraints should be addressed before attributing passage failure to light or implementing a lighting retrofit.

## 7. CONCEPTUAL MODEL OF DARKNESS-RELATED PASSAGE

The reviewed evidence supports a stage-based conceptual model in which darkness influences fish passage through a sequence of behavioural responses rather than through a single binary response. Passage through an enclosed structure can be divided into five stages:

**Approach → Entry → Transit → Completion**

At each stage, a fish may proceed, delay, retreat, select an alternative route, or fail to complete passage. Following entry, fish may pause or remain within the structure, reverse direction, or leave through the entrance without completing passage. The influence of darkness may differ among stages and may even change direction within the same passage event. Consequently, successful entry does not necessarily imply successful passage, and delayed entry does not necessarily indicate that a fish will experience slow transit once inside the structure.

### 7.1 APPROACH

The approach stage begins when a fish encounters the hydraulic, structural, and visual influence of the crossing. At this stage, the fish may detect the culvert opening, attraction flow, a change in water velocity, overhead cover, or a contrast between exterior and interior illumination. These cues influence whether the fish continues toward the entrance, delays nearby, or moves away.

Approach responses are likely to depend strongly on visual ecology and movement motivation. Diurnally active and schooling fishes may rely on visual information to maintain orientation or cohesion and may be less willing to approach a darkened route (Kemp et al. 2005; Keep et al. 2021). Nocturnal or negatively phototactic fishes may show the opposite response and avoid illuminated routes rather than darkness itself (Vowles and Kemp 2021). Hydraulic cues can also attract or repel fish before they reach the entrance, making it difficult to attribute approach behaviour to light alone.

Alternative routes are particularly important at this stage. In experimental choice systems, fish could reject a covered, structurally complex, or illuminated channel and select another route (Kemp et al. 2005; Kemp and Williams 2008; Vowles and Kemp

2021). In a road culvert with no nearby alternative, the same response might instead appear as delay, retreat, or entry and subsequent exit.

### 7.2 ENTRY

Entry represents the transition from the exterior environment into the enclosed structure. The visual contrast at the opening, aperture size, flow transition, and degree of enclosure may be particularly influential at this stage.

Several studies indicate that darkness can reduce or delay entry. Adult salmonids hesitated more before entering the darkened fishway examined by Long (1959). Australian Smelt and Fly-specked hardyhead made fewer entries into darkness at low illuminance in Keep et al. (2021), and natural light accelerated entry into the pipe-fishway apparatus used by Kammanankada et al. (2026). Overhead cover also reduced entry or passage rate for some species in Tarena et al. (2025).

However, entrance responses cannot be attributed to absolute light level alone. Long's fish encountered a narrow dark opening, while Slatick (1970) found that a tapered entrance improved entry into a small-diameter pipe without altering interior lighting. Attraction flow, entrance geometry, and trapping configuration also influenced entry in Kammanankada et al. (2026). The entrance therefore represents an integrated sensory and structural transition rather than a simple boundary between light and darkness.

Evidence for mitigating abrupt light transitions was inconclusive. Slatick (1970) found no measurable difference between abrupt and gradual transitions into a nonilluminated 0.9 m pipe for the adult salmonids tested. This result does not exclude effects for smaller or more strongly diurnal fishes, but it indicates that entrance contrast alone is not consistently limiting.

### 7.3 TRANSIT

Transit begins after a fish has entered the structure and includes movement through its interior. Darkness may affect swimming speed, schooling, orientation, station-holding, responsiveness to hydraulic cues, and willingness to continue.

The effect of darkness during transit was not consistently adverse. Long (1959) found that fish entered more slowly in darkness but traversed the fishway substantially faster once inside. Similarly, Vowles et al. (2014) found that juvenile Chinook Salmon were less likely to detect and avoid an accelerating hydraulic gradient in darkness, reducing avoidance-related delay. In these cases, reduced visual information accelerated transit by limiting assessment or rejection of downstream conditions.

Other studies found slower or less active movement in darkness. Juvenile salmonids formed fewer schools, approached experimental structures less often, and showed altered orientation and swimming behaviour when visual cues were unavailable (Kemp et al. 2006; Kemp and Williams 2008, 2009). Slatick (1970) found that illumination substantially accelerated transit by steelhead and fall Chinook Salmon, although effects were weaker or reversed for other salmonids.

Structure length, turns, hydraulic gradients, depth, and resting opportunities modify these responses. Slatick (1970) found that turns delayed passage and that velocity, diameter, and water depth influenced transit. Amtstaetter et al. (2017) demonstrated that young galaxiids traversed a long section of complete darkness after baffles reduced hydraulic challenge and provided resting opportunities. Darkness during transit therefore cannot be interpreted independently of the physical conditions encountered within the crossing.

### 7.4 COMPLETION

Completion occurs when a fish emerges from the opposite upstream or downstream end of the passage structure. Passage completion is often the most management-relevant endpoint, but it does not reveal where or why passage failed.

Lighting sometimes altered completion substantially. In Slatick (1970), illumination increased steelhead completion from 55% to 98%. Jones et al. (2017) recorded substantially fewer upstream-moving native fishes under low-light and dark treatments than under daylight or artificial illumination. Artificial light at night reduced passage success by European Gudgeon in Tarena et al. (2024).

In contrast, completion by fall Chinook Salmon and Sockeye Salmon was nearly unchanged between illuminated and nonilluminated conditions in Slatick (1970), while summer Chinook Salmon and Coho Salmon sometimes completed passage more frequently without illumination. Fish moved through the low-light box culverts examined by Kozarek et al. (2017), although passage appeared partially limited in the two longer structures for some groups and the independent influence of lighting could not be determined. Amtstaetter et al. (2017), more directly, documented successful passage through a completely dark 70 m culvert after hydraulic remediation. These results reinforce that darkness can reduce completion for particular species and contexts without constituting a universal barrier.

Completion is also sensitive to the observation period. A fish classified as unsuccessful within a short experimental trial might pass after a longer delay under natural conditions. Conversely, a fish detected near the end of a structure may not necessarily have exited successfully. Passage studies should therefore report both the monitoring duration and the criteria used to define completion.

### 7.5 RETENTION AND UNSUCCESSFUL EXIT AFTER ENTRY

Exit (passage failure, return to entry) and retention (holding or reduced movement rate within structure) were the two least frequently measured stages in the reviewed literature. This is an important limitation because lighting may encourage entry without supporting continued movement or successful emergence from the structure.

Kammanankada et al. (2026) provided the clearest example. Localized artificial-light treatments produced relatively high entry into the pipe apparatus, but approximately 95–98% of fish subsequently exited. A treatment could therefore appear effective when

assessed using entry alone but ineffective when retention or progression through the pipe was considered.

Conditions near the outlet may also influence whether fish complete passage or exit the structure. Outlet drops, turbulence, excessive velocity, abrupt changes in light, and a lack of suitable receiving habitat may prevent successful passage. These factors were not consistently evaluated in darkness studies, and relatively little is known about whether a transition from darkness into bright light affects exit behaviour.

### 7.6 FACTORS MODIFYING PASSAGE AT EACH STAGE

The influence of darkness across the passage sequence can be modified by several interacting and non-mutually exclusive factors:

- **Species visual ecology:** dependence on vision, spectral sensitivity, diel activity, phototaxis, shoaling tendency, and use of non-visual senses;
- **Life stage:** body size, swimming capacity, sensory development, predator vulnerability, and experience;
- **Movement direction and motivation:** upstream versus downstream movement, directed migration versus resident movement, and strength of seasonal motivation;
- **Diel and seasonal context:** prevailing ambient light, naturally preferred movement periods, seasonal run timing, and physiological condition;
- **Exterior and interior illumination:** absolute light level, spectrum, spatial distribution, and contrast at the openings;
- **Structure characteristics:** length, aperture, diameter, alignment, turns, overhead cover, and availability of alternative routes;
- **Hydraulic conditions:** velocity, depth, turbulence, acceleration, attraction flow, and resting opportunities;
- **Environmental modifiers:** temperature, aperture, visual contrast, water clarity, and prior exposure;
- **Other sensory cues:** substrate, sound, lateral-line information, olfactory cues, and social information from conspecifics.

These modifiers do not act independently. For example, the absence of visual information may reduce the ability of a downstream migrant to detect an accelerating velocity gradient, while the same darkness may increase entry hesitation by a diurnally active upstream migrant. A small aperture may intensify the perception of darkness and enclosure, whereas a large opening may permit greater natural light and provide a less abrupt structural transition. Strong migratory motivation may also enable fish to persist through conditions that would cause avoidance during routine resident movements.

### 7.7 INTEGRATED INTERPRETATION

The stage-based model helps reconcile results that might otherwise appear contradictory. Darkness may:

- delay approach or entry but accelerate transit after entry, as observed by Long (1959);
- reduce visual avoidance of hydraulic conditions and thereby shorten delay, as observed by Vowles et al. (2014);
- increase entry under artificial illumination but also increase subsequent exit, as observed by Kammanankada et al. (2026);
- have little effect on completion when hydraulic conditions are suitable, as observed in several culvert and pipe studies;
- reduce passage for visually oriented species while artificial illumination may deter nocturnal or negatively phototactic species.

Accordingly, darkness-related passage should not be evaluated using a single endpoint whenever multiple stages can be observed. At minimum, studies and monitoring programs should distinguish whether fish:

1. approached the structure;
2. entered;
3. progressed through the interior;
4. completed passage; and
5. remained beyond the structure or returned.

The model also suggests that the term *behavioural barrier* should be applied with care. Darkness may represent a complete barrier in a particular setting, but the available literature more commonly documents changes in passage probability, timing, route choice, or persistence. In most cases, it is more precise to describe darkness as a factor that can create behavioural resistance or partial passage limitation, the magnitude of which depends on the species, passage stage, environmental context, and physical characteristics of the structure.

## 8. STRENGTHS AND LIMITATIONS OF THE EVIDENCE

The evidence base was sufficient to establish that lighting conditions can influence fish behaviour and passage, but it was not sufficient to support universal design thresholds or a general conclusion that darkness constitutes a complete barrier. Its principal strength was the presence of controlled experiments demonstrating causal responses to darkness, illumination, or overhead cover. These studies included replicated light treatments, measurements of multiple behavioural endpoints, and, in some cases, comparisons among species exposed to the same experimental conditions (Jones et al.

2017; Keep et al. 2021; Tarena et al. 2024, 2025). Historical pipe and fishway experiments also provided direct evidence from relatively long enclosed structures and adult upstream migrants (Long 1959; Slatick 1970).

The evidence base also included complementary study designs. Laboratory and flume experiments provided strong control over lighting and hydraulic conditions, whereas field studies in culverts, pipe fishways, and operating fishways offered greater environmental realism. Together, these studies showed that darkness can influence approach, entry, transit, completion, and exit or retention, and that effects can differ among these stages. However, the balance between experimental control and direct relevance to road culverts varied substantially among studies.

## 8.1 LIMITED DIRECT EVIDENCE FROM ROAD CULVERTS

Only two Core Empirical studies used operational road culverts as their primary study setting, and neither independently manipulated lighting throughout a full-length culvert. Kozarek et al. (2017) combined field observations and mark–recapture in three box culverts with shaded laboratory passageways. In the field component, culvert length and midpoint illuminance were strongly confounded, preventing the independent effect of lighting from being determined. Amtstaetter et al. (2017) documented successful passage through a dark culvert following hydraulic remediation but did not independently manipulate darkness. A third, Supporting Empirical study, Gregory et al. (2004) included artificial lighting during short-term releases of hatchery juvenile steelhead in an actual culvert, but the treatment was ancillary, unquantified, sparsely replicated, and not analysed statistically.

Consequently, much of the evidence was derived from experimental pipes, fishways, flumes, and short channel sections. These studies provide mechanistic evidence that light can alter behaviour, but they do not fully reproduce the conditions encountered in long road culverts, including gradual light attenuation, constrained aperture, variable substrate, debris, turbulence, sound, temperature gradients, and limited alternative routes.

## 8.2 TAXONOMIC AND GEOGRAPHIC REPRESENTATION

The evidence was geographically concentrated in North America, Australia, and Europe, with one study from Asia. No Core Empirical study was conducted in Canada. Transferability to Canadian fish communities is therefore uncertain, particularly for species and life-history strategies not represented in the available literature.

Salmonids accounted for seven of the 16 Core Empirical studies. Five of the six downstream-movement studies focused on juvenile salmonids, while adult salmonids were prominent in the historical upstream-passage experiments. Small-bodied riverine fishes were also relatively well represented, particularly Australian and European cypriniform or leuciscid species. In contrast, anguillids and galaxiids were each represented by one Core Empirical study, and several important ecological groups were absent or sparsely represented.

The prominence of salmonids reflects their management importance and extensive use in fish-passage research, but limits generalization to other taxa. Salmonids also displayed substantial variation among species, life stages, and seasonal runs, demonstrating that even a comparatively well-studied taxonomic group cannot be treated as behaviourally uniform.

### 8.3 DIFFERENCES AMONG STUDY STRUCTURES

The reviewed studies included road culverts, experimental pipes, pipe-fishway entrances, vertical-slot and pool-and-overfall fishways, open flumes, choice channels, and hydraulic weirs. These structures differed markedly in length, width, aperture, hydraulic complexity, degree of enclosure, and the spatial distribution of light.

Fishways and experimental flumes often provided strong causal inference because lighting could be manipulated while other conditions were controlled. However, many were shorter, wider, or more open than road culverts and did not reproduce gradual entry into a long enclosed barrel. Conversely, field culvert studies provided high structural realism but often lacked untreated controls or independent light manipulation.

The findings should therefore be interpreted along two separate dimensions:

1. **Strength of causal inference about light**, which was greatest in controlled experiments; and
2. **Directness to culvert passage**, which was greatest in field studies of operational culverts and long pipe systems.

No single study type provided both complete experimental control and full ecological realism.

### 8.4 HETEROGENEOUS LIGHT EXPOSURES

“Darkness” was defined and produced differently among studies. Treatments included complete or near-complete darkness, reduced illuminance, overhead cover, natural light attenuation, abrupt light-to-dark boundaries, and artificial light at night. These exposures are biologically related but not interchangeable.

Overhead cover may alter perceived enclosure, predator risk, sound, and visual complexity in addition to illumination. Artificial light at night alters the natural diel environment and may repel nocturnal species even where daytime illumination could facilitate passage. A sharp transition into darkness may produce a different behavioural response than gradual attenuation along a long culvert. Combining these exposures under a single category of darkness would therefore obscure meaningful differences in mechanism.

Some studies described treatments qualitatively, while others measured illuminance. Even where lux values were reported, measurements were taken at different locations, depths, or times and using different instruments. Spectral composition was rarely

reported. Because fish visual sensitivity depends on wavelength as well as intensity, equivalent lux values do not necessarily represent equivalent biological exposures.

### 8.5 LIMITED TRANSFERABILITY OF ILLUMINANCE THRESHOLDS

Keep et al. (2021) provided the clearest quantitative relationships between illuminance and entry into darkness, but these thresholds were derived for a small number of Australian species under controlled, clear-water laboratory conditions. The experiment measured voluntary entry into a dark channel section rather than successful passage through a long culvert.

Other studies used lighting treatments ranging from fractions of a lux to several thousand lux. Historical experiments used especially bright artificial illumination. Slatick (1970) reported approximately 3,455 lx at the bottom of an empty illuminated pipe, while Long (1959) used approximately 3,229–10,764 lx at the water surface. These treatments were much brighter than many contemporary culvert-lighting proposals and may have produced behavioural responses that would not occur under lower-intensity illumination.

Available thresholds should therefore be treated as study-specific response estimates rather than transferable design criteria.

### 8.6 VARIATION IN PASSAGE ENDPOINTS

Studies differed in what they considered evidence of passage or a behavioural barrier. Reported endpoints included:

- approach;
- route choice;
- entry;
- exit after entry;
- retention ajfter entry;
- movement counts;
- passage rate;
- transit time;
- passage completion;
- schooling and orientation;
- diel timing.

These endpoints were not equivalent. Reduced entry may indicate a behavioural barrier at the entrance, but does not describe transit by fish that enter. Faster transit does not

necessarily translate into greater completion. High entry may be followed by exit, as observed by Kammanankada et al. (2026).

The diversity of endpoints was scientifically informative because it demonstrated that darkness can affect different stages in opposing directions. It also prevented calculation of a single standardized effect across the literature. Studies reporting only passage completion may have missed important delays or repeated attempts, while studies reporting entry alone may have overestimated successful passage.

### 8.7 CONFOUNDING WITH PHYSICAL AND TEMPORAL CONDITIONS

Light was frequently associated with other environmental or experimental variables. In field settings, dark culverts also differed in length, aperture, flow, depth, substrate, slope, and outlet conditions. In experiments involving overhead cover, reductions in light occurred together with increased enclosure. In Amtstaetter et al. (2017), hydraulic remediation and resting opportunities changed while darkness remained, allowing successful passage through a dark structure but not an independent estimate of the effect of darkness.

Temporal confounding was also present. Species were often tested during different migration seasons because they were available at different times. In Slatick (1970), differences between summer and fall Chinook Salmon responses could reflect seasonal run, population, motivation, or environmental conditions. In Wang et al. (2025), dark and natural-light treatments occurred sequentially rather than in a fully randomized design. Natural day–night comparisons also confounded light with time-dependent changes in activity, temperature, predation risk, and motivation.

These limitations do not invalidate the observed responses, but they reduce confidence in attributing them exclusively to light.

### 8.8 INCONSISTENT REPORTING OF ENVIRONMENTAL CONDITIONS

Hydraulic conditions were usually reported more thoroughly than optical conditions, but reporting remained inconsistent. Velocity, depth, and discharge were quantified in many experimental studies, whereas turbulence, attraction flow, and within-structure hydraulic variability were less consistently described. Turbidity and water clarity were rarely incorporated analytically, even though both affect the amount and quality of visual information available to fish.

Temperature was generally reported as a background variable but was seldom tested as an interaction with light. Similarly, few studies measured the duration of visual acclimation, prior exposure to dark structures, or repeated passage experience. The absence of standardized reporting limits comparisons among studies and prevents evaluation of whether apparent differences arose from species traits or unmeasured environmental conditions.

## 8.9 UNRESOLVED HISTORICAL EVIDENCE

Several historical reports have been repeatedly cited as evidence that fish pass through long dark culverts or tunnels. Slatick (1970) and Long (1959) were retrieved and independently reviewed, substantially strengthening the evidence base.Another historical account reported passage through four long culverts (approximately 183–229 m) and concluded that darkness appeared to have little effect (Kay and Lewis 1970, as cited in Boubée et al. 1999). Because the original report was not retrieved, this observation is retained as secondary-only evidence and is not treated as independently verified.

Other tunnel studies were also identified through secondary sources but were not included as Core Empirical evidence because they did not isolate darkness experimentally or because the original reports were not reviewed. These accounts provide useful context but cannot resolve the effect of darkness independently from hydraulics, migration motivation, or passage opportunity.

## 8.10 OVERALL STRENGTH OF INFERENCE

Despite these limitations, several conclusions were supported consistently across multiple study types. Controlled experiments demonstrate that fish detect and respond behaviourally to changes in light, and that these responses can influence passage. Multiple studies also show that effects vary among species, life stages, movement directions, and passage stages. Evidence is similarly strong that physical and hydraulic conditions modify or sometimes dominate responses attributed to darkness.

Confidence is lower where the evidence would need to support universal conclusions. Successful passage through dark structures shows that darkness is not necessarily an absolute barrier, but does not demonstrate that darkness has no behavioural cost. Conversely, avoidance or delay in experimental channels does not establish that an operational culvert will be impassable. Table 3 summarizes our confidence in each of the principal synthesis conclusions, along with the basis for that assessment.

Table 3: Confidence in principal synthesis conclusions.

| Synthesis conclusion | Confidence | Basis for assessment |
|---|---|---|
| Darkness and reduced illumination can alter fish passage behaviour | **High** | Demonstrated in multiple controlled studies using entry, route choice, passage rate, delay, schooling, and completion endpoints |
| Darkness is a universal or complete barrier to fish passage | **Low; unsupported** | Multiple taxa passed through completely dark culverts, pipes, and fishways |
| Darkness can create partial resistance through delay, avoidance, retreat, or increased exit occurrence | **High** | Consistent evidence across experimental channels, fishways, pipes, and some culvert studies |
| Responses vary among species, ecological guilds, life stages, and movement contexts | **High** | Contrasting responses occurred within shared experiments and even among salmonid species or seasonal runs |
| Artificial interior lighting universally improves passage | **Low; unsupported** | Lighting produced beneficial, neutral, and adverse responses and sometimes improved one endpoint while worsening another |
| Maintaining natural light benefits visually oriented fishes | **Moderate** | Supported by several experiments, but few full-length culvert evaluations |
| Abrupt light transitions are a general barrier | **Low** | Entrance hesitation was observed in some studies, but Slatick found no difference between abrupt and gradual transitions |
| Hydraulic and structural conditions modify light-related responses | **High** | Demonstrated through velocity gradients, baffles, pipe diameter, entrance geometry, depth, turns, and attraction flow |
| Specific lux thresholds can be broadly transferred among species and culverts | **Low** | Threshold evidence was limited to a few species and controlled conditions; spectrum and field conditions were poorly represented |
| Evidence can presently support a universal culvert-lighting standard | **Low** | Insufficient direct road-culvert experiments and substantial species and context dependence |

Overall, the evidence is strongest for the conclusion that darkness is a biologically relevant environmental condition capable of modifying passage behaviour. It is substantially weaker for predicting when that response becomes a consequential barrier at a particular culvert. The available studies support conditional, species- and site-specific assessment rather than a universal threshold based solely on culvert length or interior illuminance.

# 9. IMPLICATIONS FOR ASSESSMENT AND REGULATION

The reviewed evidence does not support treating culvert darkness as either automatically harmless or inherently impassable. Darkness can influence approach, entry, transit, passage completion, and retention, but its effects vary among species, life stages, movement directions, environmental conditions, and crossing designs. Assessment should therefore be conditional and evidence based, with darkness considered alongside the hydraulic and structural characteristics of the crossing rather than as an independent pass–fail criterion.

## 9.1 INTERPRETING DARKNESS AS A POTENTIAL BEHAVIOURAL BARRIER

Darkness alone should not be assumed to prevent fish passage. Adult salmonids and juvenile galaxiids successfully traversed long sections of complete or near-complete darkness, and some species showed neutral or improved movement under dark conditions (Long 1959; Slatick 1970; Amtstaetter et al. 2017; Kozarek et al. 2017; Wang et al. 2025). Conversely, controlled studies showed that low light, darkness, or overhead cover can reduce entry, increase delay, alter route choice, or lower passage rates for some fishes (Jones et al. 2017; Keep et al. 2021; Tarena et al. 2025).

The appropriate regulatory question is therefore not simply whether a culvert is dark, but whether reduced light is likely to cause a biologically meaningful change in passage by the species and life stages of concern. Relevant effects may include:

- fewer fish approaching or entering the structure;
- longer delays before entry or completion;
- repeated retreat or route rejection;
- reduced passage probability;
- altered timing of migration;

A behavioural effect need not completely prevent passage to be ecologically relevant. Delays may increase energetic costs, exposure to predators, displacement from preferred migration periods, or the likelihood that fish encounter unsuitable flows or temperatures. However, the present evidence does not provide general thresholds for determining when a delay or reduction in passage becomes consequential at the population level.

## 9.2 CONFIRMING HYDRAULIC AND STRUCTURAL PASSABILITY

Behavioural assessment is most informative when the crossing is otherwise expected to be physically passable. Excessive velocity, inadequate depth, turbulence, outlet drops, small aperture, poor entrance conditions, or a lack of resting opportunities can independently impede passage and may dominate any effect of light.

Several studies demonstrated that passage through dark structures improved when hydraulic or structural conditions were remediated. Young galaxiids traversed a 70 m dark culvert after baffles reduced the hydraulic challenge and provided resting opportunities (Amtstaetter et al. 2017). Slatick (1970) found strong effects of pipe diameter, entrance geometry, velocity, depth, and turns. Gregory et al. (2004) documented responses of hatchery juvenile steelhead to baffle configurations, whereas ancillary artificial-light trials produced no apparent change in movement but were not analysed statistically.

Accordingly, an assessment should first determine whether:

1. water velocity and turbulence are within the capabilities of the target fish;
2. sufficient depth and suitable water-surface conditions are maintained;
3. the inlet and outlet are accessible;
4. entrance geometry and attraction flow allow fish to locate and enter the structure;
5. resting opportunities are available where needed; and
6. debris, sediment, damage, or maintenance conditions do not create additional impediments.

Where these conditions are not met, attributing poor passage to darkness would be premature. Darkness-specific assessment becomes most relevant after physical and hydraulic constraints have been addressed or reasonably excluded.

## 9.3 CONSIDERING THE TARGET FISH ASSEMBLAGE

The target species, ecological guild, life stage, movement direction, and diel behaviour should guide the level and type of assessment. The reviewed studies indicate that responses cannot be generalized across the fish community.

Greater concern may be warranted where the target assemblage includes:

- diurnally active, visually oriented species;
- schooling water-column fishes that depend on visual cues;
- small-bodied fishes showing strong light preference;
- life stages with limited experience entering enclosed structures;
- species for which passage must occur during bright daytime conditions.

Different concerns apply to nocturnal or negatively phototactic species. Artificial lighting may deter these fishes even if it benefits diurnal taxa. European Eel, for example, rejected an artificially illuminated downstream route (Vowles and Kemp 2021). Assessment should therefore consider the entire fish assemblage rather than evaluating a lighting proposal solely against one target species.

Movement direction is also important. Evidence from downstream-moving salmonid smolts should not be applied uncritically to adult upstream passage. Downstream migrants may use light to detect and reject accelerating flows, whereas upstream migrants may respond more strongly to entrance contrast, attraction flow, or aperture. Resident voluntary movement may differ again from strongly motivated seasonal migration.

### 9.4 EVALUATING LONG OR HIGHLY ENCLOSED CROSSINGS

Long structures warrant closer consideration because natural light generally declines with distance from the entrance and because a fish may remain within enclosed conditions for longer. However, culvert length alone is not evidence that darkness will constitute a behavioural barrier. Fish passed through dark experimental pipes up to 82.3 m long in Slatick (1970), and young galaxiids traversed a 70 m road culvert after hydraulic remediation (Amtstaetter et al. 2017). Secondary accounts also describe passage through substantially longer enclosed structures, although these reports do not isolate the effect of darkness.

Assessment of a long crossing should therefore consider length together with:

- aperture and cross-sectional openness;
- alignment and the presence of turns;
- the rate at which light declines from the entrance;
- whether daylight is visible from within the structure;
- light contrast at structural interfaces or openings;
- flow velocity and water depth;
- availability of resting areas;
- expected transit time;
- the species and life stages requiring passage.

Measured light profiles are more informative than length alone. Measurements should describe exterior conditions, both openings, and representative positions through the structure, including the darkest section. Time of day, weather, water depth, turbidity, and the position and orientation of the light sensor should also be reported.

## 9.5 USE OF ARTIFICIAL LIGHTING

Artificial interior illumination should not be prescribed automatically as mitigation for a dark culvert. The evidence includes beneficial, neutral, and adverse responses. Artificial light improved movement by some small-bodied fishes and markedly improved steelhead passage in Slatick (1970), but slowed or reduced completion by other salmonids, deterred European Eel, and produced high exit rates in a pipe-entry experiment (Long 1959; Slatick 1970; Vowles and Kemp 2021; Kammanankada et al. 2026; summarized in Table 2).

Where artificial lighting is proposed, the assessment should consider:

- target and non-target species;
- migration direction and season;
- whether fish normally move during daylight or darkness;
- light intensity and spectral composition;
- fixture spacing and the spatial continuity of illumination;
- whether lighting creates an abrupt bright–dark boundary;
- operation during daytime, nighttime, or both;
- maintenance and reliability;
- potential attraction, avoidance, or trapping effects;
- whether fish enter but subsequently exit.

A lighting treatment should ideally be tested at the site or in a representative setting before being adopted as a permanent requirement. Controlled comparisons should include unlit conditions and measure more than initial entry. Where several species with contrasting diel ecology use the crossing, passive design measures that preserve natural light may be preferable to continuous artificial illumination, although the effectiveness of passive measures also requires site-specific evaluation.

Where overhead grates, skylights, or light wells are proposed, their contribution should be evaluated using measured underwater light profiles rather than inferred from the presence of an opening. Opening dimensions, spacing, orientation, road-deck thickness, sun angle, season, vegetation, water depth, turbidity, grate obstruction, and maintenance can all influence the light reaching the passage route. Assessment should also consider whether discrete openings create alternating bright and dark zones and whether the design introduces roadway runoff, debris, thermal changes, or additional maintenance and safety requirements. Where the consequences of impaired passage are material, monitoring should evaluate approach, entry, transit, completion, retreat, and retention rather than simply confirming that daylight enters the structure.

## 9.6 MONITORING PASSAGE AND BEHAVIOURAL RESPONSES

Monitoring should distinguish the successive stages of passage rather than relying on a single detection or count. At minimum, monitoring should determine whether fish:

1. approach the crossing;
2. enter the structure;
3. progress through the interior;
4. complete passage; and
5. remain beyond the structure rather than return.

This distinction is important because lighting can affect each stage differently. Long (1959) found slower entry but faster transit in darkness, while Kammanankada et al. (2026) observed high entry followed by high exit under localized artificial lighting. A monitoring design based only on entry would have interpreted these studies differently from one based on complete passage.

Where feasible, monitoring should include:

- counts or detection rates at the approach, entrance, interior, and endpoint;
- entry delay and total passage time;
- unsuccessful attempts and retreat;
- passage completion probability;
- day and night comparisons;
- relevant hydraulic and environmental covariates;
- species, life stage, and size;
- sufficient monitoring duration to capture delayed passage.

Comparisons between treated and untreated periods, structures, or routes are preferable to observations at a single crossing without a reference condition. Before–after monitoring can be informative, but temporal changes in flow, temperature, fish abundance, and migration timing should be considered.

## 9.7 REGULATORY INTERPRETATION

The available evidence supports a weight-of-evidence approach rather than a universal darkness threshold. Regulatory concern should increase where several lines of evidence coincide—for example, where a long, narrow structure has near-total interior darkness, strong entrance contrast, otherwise passable hydraulics, and a target assemblage dominated by diurnal or visually oriented fishes. Concern should be lower

where species-specific evidence demonstrates successful passage under comparable conditions and hydraulic and structural conditions are suitable.

A finding that fish have successfully passed a dark structure should not automatically be interpreted as evidence that darkness had no effect. Passage may still have been delayed or reduced relative to an illuminated or open condition. Conversely, laboratory avoidance of darkness should not be assumed to mean that a field culvert will be impassable, particularly where the experimental study involved a different species, life stage, movement direction, or structure.

Pending stronger evidence, regulatory conclusions could be framed using the following principles:

- Darkness is a potential modifier of passage, not a presumed absolute barrier.
- Hydraulic and structural passability should be evaluated first.
- Assessment should be specific to the target species, life stage, movement direction, and migration period.
- Passage success and behavioural delay should be considered separately.
- Culvert length should trigger closer evaluation where appropriate, but should not serve as a stand-alone barrier criterion.
- Artificial lighting should be evaluated as a species- and site-specific intervention, not a default mitigation measure.
- Passive daylighting features may be considered where long enclosed crossings are unavoidable, but they should not be credited as effective mitigation without confirming the resulting light environment and, where warranted, monitoring fish passage.
- Monitoring should distinguish approach, entry, transit, and completion, and document retention within the structure and unsuccessful exit through the entrance
- Uncertainty should be stated explicitly where evidence is transferred from fishways, flumes, or non-local species.

These principles provide the basis for a future decision framework. Such a framework could be used to determine when a standard hydraulic assessment is sufficient, when additional characterization of interior light is warranted, when targeted behavioural monitoring should be required, and when an experimental mitigation trial would be more appropriate than a prescriptive lighting standard.

# 10. KNOWLEDGE GAPS AND RESEARCH PRIORITIES

Although the available literature demonstrates that darkness can influence fish behaviour and passage, the evidence remains insufficient to predict when reduced light will constitute a consequential barrier at a particular culvert. Future research should prioritize studies that improve direct applicability to road crossings, isolate the mechanisms underlying observed responses, evaluate realistic mitigation measures, and adopt more consistent monitoring and reporting practices.

## 10.1 EVIDENCE GAPS

The most important evidence gap is the limited number of controlled studies conducted in operational road culverts. Only a small proportion of the Core Empirical literature examined full-length culverts, and none independently manipulated illumination throughout a long road crossing while controlling hydraulic and structural conditions. Much of the existing evidence instead comes from fishways, experimental pipes, flumes, and short channel sections. These studies are valuable for identifying behavioural mechanisms but cannot fully reproduce the gradual attenuation of light, restricted aperture, acoustics, substrate, hydraulics, and limited route choice associated with long culverts.

Studies are particularly needed in long road culverts representative of those encountered during regulatory review. Research should encompass a range of lengths, diameters, shapes, alignments, and entrance conditions and should measure interior light profiles rather than relying on culvert length as a proxy for darkness. Comparison among structures should also account for velocity, depth, slope, outlet condition, substrate, resting opportunities, and attraction flow.

No Core Empirical study was conducted in Canada. The evidence base is dominated by studies from the United States, Australia, and Europe, and its applicability to Canadian fish communities remains uncertain. Canadian studies should include species and assemblages of direct regulatory relevance, particularly those occupying boreal, Arctic, montane, and prairie systems.

Additional research is needed on non-salmonid fishes. Salmonids were the most frequently studied group, particularly as juvenile downstream migrants and adult upstream migrants. Small-bodied Australian and European fishes were also represented, but evidence remains limited for many benthic, nocturnal, nonschooling, warmwater, and northern species. The range of visual systems, diel behaviours, and movement strategies among fishes makes broad extrapolation from salmonids or a small number of cypriniform species inappropriate.

Threatened and endangered fishes may warrant particular attention where culvert crossings could affect access to limited spawning, rearing, refuge, or overwintering habitat. Direct experimentation may be constrained by animal availability and conservation concerns, but carefully designed observational studies, controlled choice

experiments, non-invasive telemetry, and the use of ecologically similar surrogate species could improve the evidence available for regulatory decisions.

Multiple-species field studies should be prioritized because most crossings are used by assemblages rather than a single target species. A lighting treatment that benefits a diurnal, visually oriented fish may deter a nocturnal or negatively phototactic species. Studies should therefore examine community-level responses and determine whether mitigation changes assemblage composition, timing of movement, or relative passage success among taxa.

### 10.2 MECHANISTIC GAPS

Further research is needed to distinguish the effect of absolute interior light level from the effect of contrast at the entrance. Fish may respond to complete darkness, to a rapid decline in illumination, to the apparent aperture of the opening, or to the combined transition from an open channel into a confined structure. Long (1959) observed hesitation at a narrow dark entrance, whereas Slatick (1970) found no measurable difference between abrupt and gradual transitions into a larger pipe. Experiments that independently manipulate interior illuminance, entrance contrast, and aperture would help determine which component drives avoidance or delay.

Visual adaptation and acclimation time are also poorly understood. Fish approaching a long culvert may experience a gradual reduction in light and adapt as they proceed, whereas many experiments imposed an abrupt transition between bright and dark treatments. Future studies should quantify the time required for fish to adapt to reduced illumination, test whether slower transitions affect entry or transit, and distinguish short-term visual adaptation from learning through repeated exposure.

Spectral sensitivity represents another major uncertainty. Most studies reported illuminance in lux, which is weighted according to human visual sensitivity and may not accurately represent the light perceived by fish. Species differ in retinal structure, spectral sensitivity, developmental stage, and adaptation to local water colour. Future studies should report light spectrum, wavelength distribution, colour temperature, fixture type, and underwater irradiance alongside lux measurements. Where possible, exposures should be expressed using biologically relevant measures linked to the visual sensitivity of the target species.

Interactions between light, turbidity, and hydraulics are difficult to disentangle and require controlled investigation. Turbidity reduces visual range and changes spectral composition, potentially making a nominal lux value biologically different among streams. Hydraulic conditions may also alter the importance of visual cues. Darkness can reduce the ability of fish to detect accelerating flow, structural complexity, or alternative routes, which may either facilitate passage by reducing avoidance or impair it by reducing orientation (Kemp and Williams 2008, 2009; Vowles et al. 2014). Factorial experiments manipulating light together with velocity, turbulence, depth, and structural

complexity would provide a stronger basis for predicting responses under field conditions.

### 10.3 MITIGATION GAPS

Controlled field evaluations of artificial interior lighting are needed before lighting can be recommended as a routine culvert retrofit. Existing evidence includes beneficial, neutral, and adverse responses, and several experiments used light intensities or configurations that differ substantially from realistic field installations. Future trials should compare untreated and illuminated conditions within the same structure and evaluate different intensities, spectra, fixture spacings, and operating periods.

Artificial-light experiments should measure consequences for both target and non-target species. Particular attention should be given to nocturnal and negatively phototactic fishes, downstream migrants, predators, prey, and invertebrates. Studies should also determine whether illumination changes migration timing, attracts fish into unsuitable hydraulic conditions, concentrates fish near entrances, or increases predation risk.

Passive daylighting measures have strong conceptual appeal but require direct field evaluation. Potential measures include larger apertures, shorter or straighter alignments, open-sky sections, overhead grates, grated access covers, light wells, skylights, translucent components, and avoidance of unnecessary overhead cover. Future studies should compare passage before and after installation or between otherwise comparable treated and untreated structures; quantify the longitudinal and underwater distribution of light; evaluate opening size, spacing, orientation, season, turbidity, and obstruction; and separate the effects of increased illumination from simultaneous changes in aperture, hydraulics, or resting opportunities. Passage responses should be assessed across multiple behavioural stages and for target and non-target species with contrasting diel and visual ecologies.

Transition-zone designs also require direct testing. Entrance shading, progressive illumination, and acclimation zones are sometimes proposed to reduce abrupt contrast, but Slatick (1970) found no benefit of gradual transitions for the adult salmonids tested. Future studies should determine whether such measures benefit smaller, more strongly diurnal, or less motivated fishes and whether shading the exterior approach inadvertently reduces attraction to the opening.

Potential unintended attraction and exclusion effects should be considered explicitly. A treatment may attract fish into a structure but fail to support continued movement, as suggested by the high exit rates observed during the limited artificial-light trials of Kammanankada et al. (2026). Conversely, lighting intended to assist one species may exclude another. Mitigation studies should therefore evaluate entry, continued progression, completion, retreat, and post-passage retention across the fish assemblage.

### 10.4 MEASUREMENT AND REPORTING GAPS

A recurring weakness in the literature was the failure to distinguish among successive stages of passage. Studies often reported entry, detection within a structure, or passage completion as a single outcome. However, darkness may delay entry while accelerating transit, or artificial lighting may increase entry while also increasing retreat. Future monitoring should separately quantify:

1. approach to the crossing;
2. entry into the structure;
3. progression through the interior;
4. unsuccessful attempts (exit);
5. complete passage; and
6. persistence beyond the endpoint opening.

Time-based measures should include delay before entry, transit time after entry, total passage time, and the duration of the monitoring window. Reporting only successful fish can underestimate behavioural resistance by excluding individuals that approached but did not enter or that entered and retreated.

Light reporting should be standardized. Studies should document the instrument used, sensor orientation, measurement depth, time of day, weather, exterior illumination, entrance illumination, interior spatial profile, minimum and maximum values, spectrum, and the presence of artificial light at the opposite opening. Water depth, turbidity, substrate, and surface reflection should also be reported because they affect the underwater light environment.

Controlled comparisons are needed wherever feasible. Many field studies lacked untreated reference structures or before-and-after comparisons, while some experimental treatments were confounded with season, study site, species availability, or sequential treatment periods. Randomized or alternating treatments, reference routes, before–after–control–impact designs, and repeated measurements across flow and light conditions would strengthen causal inference.

Finally, unsuccessful passage attempts require more attention. Fish that never enter a detection zone are often absent from the dataset, making it difficult to distinguish low abundance from avoidance. Video, imaging sonar, PIT arrays, acoustic telemetry, or other technologies should be configured to capture approach, hesitation, repeated attempts, retreat, and route selection rather than only successful completion.

## 11. CONCLUSIONS

Darkness and reduced illumination can influence fish movement and passage, including approach, entry, route choice, transit time, completion, and retention. However, the evidence does not support darkness as a universal or consistently directional barrier.

Fish from several taxa successfully traversed completely dark culverts, pipes, and fishways, while other species exhibited avoidance, delay, reduced movement, or lower passage probability under low-light conditions.

Responses varied substantially among species, ecological guilds, life stages, movement directions, diel and seasonal contexts, and passage endpoints. Diurnal and visually oriented fishes were often more reluctant to enter darkened areas, whereas nocturnal or negatively phototactic fishes could be deterred by artificial illumination. Even within salmonids, responses differed among species, life stages, seasonal runs, and upstream versus downstream migrants.

Artificial lighting improved passage for some fishes but was neutral or detrimental for others and sometimes affected entry, transit, and completion in different directions. It therefore cannot currently be recommended as a universal mitigation measure. Passive maintenance of natural light, including the use of light wells, skylights, or grated openings, is a reasonable design consideration, but the effectiveness of these measures for improving fish passage has not been directly quantified.

For assessment and regulatory purposes, darkness is best treated as a potential source of behavioural resistance rather than a presumed complete barrier. Evaluation should be species- and context-specific, distinguish the successive stages of passage, and consider lighting together with the hydraulic and structural properties of the crossing. The present evidence does not support a universal illuminance or culvert-length threshold for identifying a behavioural barrier.

## ACKNOWLEDGEMENTS

We thank the three peer reviewers for their helpful comments and suggestions.

## REFERENCES

Amtstaetter, F., O'Connor, J., Borg, D., Stuart, I., and Moloney, P. 2017. Remediation of upstream passage for migrating *Galaxias* (Family: Galaxiidae) through a pipe culvert. Fish. Manag. Ecol. 24(3): 186–192. https://doi.org/10.1111/fme.12211.

Bassi, A., Love, O.P., Cooke, S.J., Warriner, T.R., Harris, C.M., and Madliger, C.L. 2022. Effects of artificial light at night on fishes: a synthesis with future research priorities. Fish Fish. 23(3): 631–647. https://doi.org/10.1111/faf.12638.

Boubée, J.A.T., Jowett, I.G., Nichols, S., and Williams, E.K. 1999. Fish passage at culverts: a review, with possible solutions for New Zealand indigenous species. Department of Conservation, Wellington, New Zealand. 63 p. + appendices.

DFO. 2007. Practitioners guide to fish passage for DFO habitat management staff. Version 1.1. Fisheries and Oceans Canada. DFO/2007-1284E. 16 p. + appendices.

DFO. 2015. Guidelines for the design of fish passage for culverts in Nova Scotia. Fisheries Protection Program, Maritimes Region, Fisheries and Oceans Canada. Cat. No. Fs104-34/2014E-PDF. 95 p.

DFO. 2016. Guidelines for watercourse crossings in Quebec. Fisheries and Oceans Canada, Quebec Region. 73 p. + appendices.

DFO. 2022a. Best management practices for the protection of freshwater fish habitat in Newfoundland and Labrador. Fisheries and Oceans Canada, St. John's, N.L. vi + 80 p.

DFO. 2022b. Code of practice: culvert maintenance. Fisheries and Oceans Canada. Cat. No. Fs23-708/4-2023E-PDF. ISBN 978-0-660-48556-0. 4 p.

Eggers, F., Schiavon, A., Calles, O., Watz, J., Comoglio, C., Candiotto, A., and Nyqvist, D. 2025. Fish behaviour in a vertical slot fishway: multi-species upstream passage success, size selectivity and diel passage patterns in a large Italian river. River Res. Appl. 41(4): 849–863. https://doi.org/10.1002/rra.4409.

Franklin, P., Baker, C., Gee, E., Bowie, S., Melchior, M., Egan, E., Aghazadegan, L., and Vodjansky, E. 2024. *New Zealand Fish Passage Guidelines*. 2nd ed. NIWA Client Report No. 2024157HN. National Institute of Water & Atmospheric Research Ltd., Hamilton, New Zealand. Version 2.03, July 2025.

Franklin, P.A., and Bartels, B. 2012. Restoring connectivity for migratory native fish in a New Zealand stream: effectiveness of retrofitting a pipe culvert. Aquat. Conserv. Mar. Freshw. Ecosyst. 22(4): 489–497. https://doi.org/10.1002/aqc.2232.

Gregory, S., McEnroe, J., Klingeman, P., and Wyrick, J. 2004. Fish passage through retrofitted culverts: final report. SPR No. 325; FHWA-OR-RD-05-05. Oregon Department of Transportation and Federal Highway Administration.

Hotchkiss, R.H., and Frei, C.M. 2007. Design for fish passage at roadway-stream crossings: synthesis report. U.S. Department of Transportation, Federal Highway Administration, McLean, Va. Report No. FHWA-HIF-07-033. 280 p.

Jones, M.J., Baumgartner, L.J., Zampatti, B.P., and Beyer, K. 2017. Low light inhibits native fish movement through a vertical-slot fishway: implications for engineering design. Fish. Manag. Ecol. 24(3): 177–185. https://doi.org/10.1111/fme.12205.

Jones, M.J., and Hale, R. 2020. Using knowledge of behaviour and optic physiology to improve fish passage through culverts. Fish Fish. 21(3): 557–569. https://doi.org/10.1111/faf.12446.

Kammanankada, H.R., Martino, J.C., Slavich, E., Suthers, I.M., and Felder, S. 2026. Improving the entrance of wild fish into pipe fishways. Can. J. Fish. Aquat. Sci. 83: 1–14. https://doi.org/10.1139/cjfas-2025-0246.

Kanno, Y., Locklear, M.L., Platis, N.M., and Lewis, S.T. 2023. Body condition metrics explain fish movement in experimental streams. J. Zool. 320(1): 18–28. https://doi.org/10.1111/jzo.13049.

Keep, J.K., Watson, J.R., Cramp, R.L., Jones, M.J., Gordos, M.A., Ward, P.J., and Franklin, C.E. 2021. Low light intensities increase avoidance behaviour of diurnal fish

species: implications for use of road culverts by fish. J. Fish Biol. 98(3): 634–642. https://doi.org/10.1111/jfb.14604.

Kemp, P.S., Gessel, M.H., and Williams, J.G. 2005. Seaward migrating subyearling Chinook salmon avoid overhead cover. J. Fish Biol. 67(5): 1381–1391. https://doi.org/10.1111/j.0022-1112.2005.00833.x.

Kemp, P.S., Gessel, M.H., Sandford, B.P., and Williams, J.G. 2006. The behaviour of Pacific salmonid smolts during passage over two experimental weirs under light and dark conditions. River Res. Appl. 22(4): 429–440. https://doi.org/10.1002/rra.913.

Kemp, P.S., and Williams, J.G. 2008. Response of migrating Chinook salmon (*Oncorhynchus tshawytscha*) smolts to in-stream structure associated with culverts. River Res. Appl. 24(5): 571–579. https://doi.org/10.1002/rra.1140.

Kemp, P.S., and Williams, J.G. 2009. Illumination influences the ability of migrating juvenile salmonids to pass a submerged experimental weir. Ecol. Freshw. Fish 18(2): 297–304. https://doi.org/10.1111/j.1600-0633.2008.00347.x.

Kozarek, J., Hatch, J., and Mosey, B. 2017. Culvert length and interior lighting impacts to Topeka Shiner passage. Minnesota Department of Transportation Final Report MN/RC 2017-44. Minnesota Department of Transportation, St. Paul, Minn. 94 p.

Long, C.W. 1959. Passage of salmonids through a darkened fishway. U.S. Fish and Wildlife Service Special Scientific Report—Fisheries No. 300. 9 p.

MacDonald, J.I., and Davies, P.E. 2007. Improving the upstream passage of two galaxiid fish species through a pipe culvert. Fish. Manag. Ecol. 14(3): 221–230. https://doi.org/10.1111/j.1365-2400.2007.00546.x.

Marchesan, M., Spoto, M., Verginella, L., and Ferrero, E.A. 2005. Behavioural effects of artificial light on fish species of commercial interest. Fish. Res. 73(1–2): 171–185. https://doi.org/10.1016/j.fishres.2004.12.009.

New Zealand Transport Agency. 2013. *Proposed designation conditions for hearing opening: Christchurch Southern Motorway Stage 2 and Main South Road Four Laning*. 1 July 2013. 62 p.

Reebs, S.G. 2002. Plasticity of diel and circadian activity rhythms in fishes. Rev. Fish Biol. Fish. 12(4): 349–371. https://doi.org/10.1023/A:1025371804611.

Slatick, E. 1970. Passage of adult salmon and trout through pipes. U.S. Fish and Wildlife Service Special Scientific Report—Fisheries No. 592. iii + 18 p.

Tarena, F., Comoglio, C., Candiotto, A., and Nyqvist, D. 2024. Artificial light at night affects fish passage rates in two small-sized Cypriniformes fish. Ecol. Freshw. Fish 33(3): e12766. https://doi.org/10.1111/eff.12766.

Tarena, F., Comoglio, C., Spairani, M., Candiotto, A., Ashraf, M.U., Abbà, M., Ruffino, C., and Nyqvist, D. 2025. Passage performance of three small-sized fish species in a vertical slot fishway with and without overhead cover. Ecol. Eng. 219: 107713. https://doi.org/10.1016/j.ecoleng.2025.107713.

Vowles, A.S., Anderson, J.J., Gessel, M.H., Williams, J.G., and Kemp, P.S. 2014. Effects of avoidance behaviour on downstream fish passage through areas of accelerating flow when light and dark. Anim. Behav. 92: 101–109. https://doi.org/10.1016/j.anbehav.2014.03.006.

Vowles, A.S., and Kemp, P.S. 2021. Artificial light at night (ALAN) affects the downstream movement behaviour of the critically endangered European eel, *Anguilla anguilla*. Environ. Pollut. 274: 116585. https://doi.org/10.1016/j.envpol.2021.116585.

Wang, B., Yao, F., Lv, J., Li, H., Wang, Z., Huang, Y., Chen, K., He, W., Wang, X., and Li, J. 2025. In situ study on the influence of a dark environment on the upstream behaviors of plateau fishes in fishways: a pilot study. Fishes 10(3): 136. https://doi.org/10.3390/fishes10030136.