

Refuge identification as a climate adaptation strategy to promote fish persistence during drought

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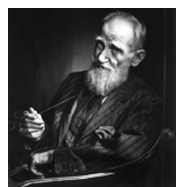
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Abstract

Climate change is leading to global increases in extreme events, such as drought, that threaten the persistence of freshwater biodiversity. Identification and management of drought refuges, areas that promote resistance and resilience to drought, will be critical for preserving and recovering aquatic biodiversity in the face of climate change and increasing human water use. Although several reviews have addressed the effects of droughts and highlighted the role of refuges, a need remains on how to identify functional refuges that can be used in a drought management framework to support fish assemblages. We synthesize literature on drought refuges and propose a framework to identify and manage functional refuges that incorporate species physiological tolerances, behaviours and life-history strategies. Stream pools, perennial reaches and off-channel habitat were identified as important drought refuges for fish. The ability of refuges to improve species resistance and resilience to drought requires careful consideration of the biology of the target species and targeted management to promote persistence, quality and connectivity of refuges. Case studies illustrate that management of drought refuges can be challenging because of competing demands for water, incomplete knowledge of ecological requirements for target species and the increasing occurrence of multi-year droughts. Climate adaptation is increasingly important, and drought refuges can increase fish resistance and resilience to climate-related drought across the riverscape.

KEYWORDS

climate adaptation, extreme events, fisheries management, refugia, resilience, resistance



Ghoti papers: Ghoti aims to serve as a forum for stimulating and pertinent ideas. Ghoti publishes succinct commentary and opinion that addresses important areas in fish and fisheries science. Ghoti contributions will be innovative and have a perspective that may lead to fresh and productive insight of concepts, issues and research agendas. All Ghoti contributions will be selected by the editors and peer reviewed.

Etymology of Ghoti: George Bernard Shaw (1856–1950), polymath, playwright, Nobel Prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.

1 | INTRODUCTION

Long-term management of species' populations requires approaches designed to facilitate adaptation to rapidly changing climate conditions (Paukert et al., 2016). One approach is to rely on climate refugia, areas that are relatively buffered from contemporary climate change (Morelli et al., 2016). Refugia refers to locations where species can persist for decades or centuries while the term refuge is generally used for shorter temporal scales and refers to locations where species can persist through seasonal or yearly disturbances (Isaak & Young, 2023; Keppel & Wardell-Johnson, 2012). Refuges provide relief from extreme weather conditions and supply source populations for recolonization when favourable environmental conditions return (Magoulick & Kobza, 2003). Managing the presence of, and access to, refuge habitat within the landscape will contribute to species persistence and are critical components of refugia (Ebersole et al., 2020; Sedell et al., 1990). Identifying and evaluating the quality of refuge habitat under extreme climatic events is the first step to promote refugia as a tool for climate adaptation (Ebersole et al., 2020).

Drought is an extreme event that has substantial repercussions for freshwater ecosystems as it alters streamflow and temperature regimes, prolongs the duration of stream drying and can lead to stream fragmentation, thereby negatively affecting river function and biodiversity (Kovach et al., 2019; Sabater et al., 2018). Drought is a natural phenomenon but is projected to become more frequent and severe with moderate droughts transitioning to megadroughts under warming global temperatures and increased human water use (Williams et al., 2020). We focus on ecological drought, which is closely related to hydrologic drought and is defined as episodic reductions in water availability that affect ecosystem services and trigger socioeconomic feedbacks (Crausbay et al., 2017; Wilhite & Glantz, 1985). Fish are highly susceptible to drought, but refuges may allow persistence by buffering fish populations from declines in abundance (i.e. resistance) or providing a source of colonists when drought conditions end (i.e. resilience) (Magoulick & Kobza, 2003). For example, some coho salmon (*Oncorhynchus kisutch*) were able to survive an extreme drought with comparable survival to non-drought years due to the

presence of refuge pools (Vander Vorste et al., 2020). However, our knowledge of best methods for identifying drought refuges is limited (Yu, Rose, et al., 2022), hindering our ability to manage freshwater species in a future, drought-stressed climate.

We synthesized current knowledge on drought refuges for fish and suggested future directions that integrate drought refuges into climate adaptation management and research. To this end, we (1) characterized drought refuges for fishes, (2) described an approach for identifying drought refuges and (3) explored refuge management and its role in climate adaptation. Our goal is to explore approaches to drought refuge identification that advance refuge protection, creation and evaluation.

2 | CHARACTERIZING DROUGHT REFUGES FOR FISHES

To evaluate the current state of knowledge and characterize drought refuge for fish, we conducted a literature search. We used three sets of search terms, "drought", "drying" or "low flow" in conjunction with "fish and refug*" (All Fields), in a Web of Science search that resulted in 677 articles once duplicates were removed (conducted on 9 February 2024, Supplement 1). From the search, 167 articles were retained as relevant, and for each, we noted terminology (refuge vs. refugia), location and temporal scale of research, species of interest, refuge type and descriptive refuge characteristics.

The number of studies on fish drought refuge has increased through time with an increase from 1 to 2 a year to ≥ 3 a year starting in 2005 (Figure 1). The geographical location of research is limited, with most studies occurring in the United States (39%) and Australia (26%). We found the terms refuge and refugia were often used interchangeably and not always in concordance with accepted definitions. Most studies were conducted over 2 or fewer years, but 20% covered greater than 5 years. This temporal range, in part, reflects variation in the temporal scale of a drought from seasonal, short-term drying events to supra-seasonal droughts that last years to decades.

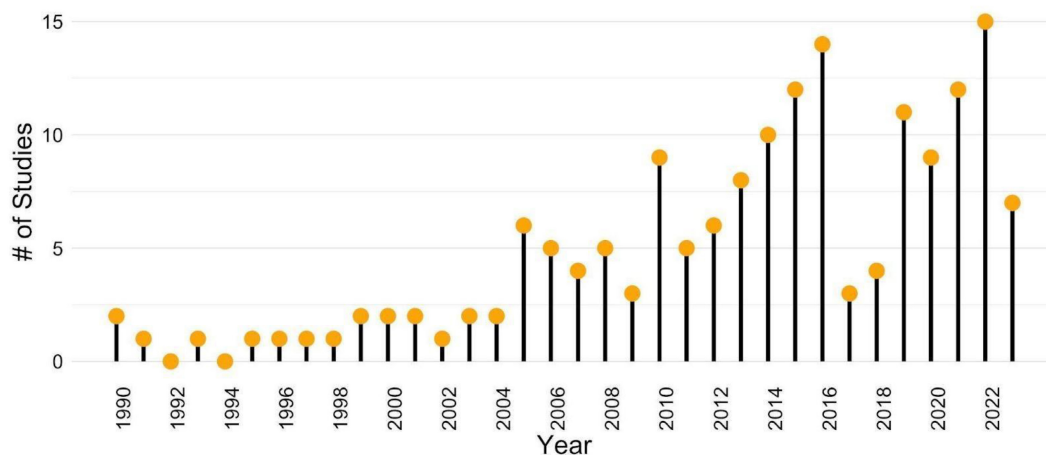


FIGURE 1 The number of studies examining drought refuges for fish by year from the literature review.

2.1 | Species of interest

The reviewed studies split relatively evenly between a focus on the entire fish assemblage (54% of studies) and individual species or subsets of species (45%). Two studies did not specifically focus on any taxa. Species studied covered a variety of taxa including popular sportfish such as coldwater brown trout (*Salmo trutta*, Salmonidae) and warmwater smallmouth bass (*Micropterus dolomieu*, Centrarchidae) and historically less-studied fishes such as upland bully (*Gobiomorphus breviceps*, Eleotridae) and creek chub (*Semotilus atromaculatus*, Cyprinidae) (Supplement 2). Minnows (families Leuciscidae and Cyprinidae) were the most examined taxon (25%) followed by Salmonids (20%), Centrarchids (9%) and Percichthyids (6%). The diverse species of interest highlight the importance of refuge habitats to fishes of differing physiological tolerances, behaviours, life-histories and reproductive strategies.

2.2 | Refuge types and environmental characteristics

The most identified refuge types were pools or deep water (59% of studies), followed by perennial, mainstem or downstream reaches (18%) and artificial habitats (e.g. ditches or reservoirs; 11%) (Figure 2).

Areas with substantial instream structure (7%), off-channel habitats (6%), groundwater springs (6%) and hyporheic zones (4%) were also noted as refuges. The environmental characteristics most attributed to refuges were flow permanence and water depth, with water quality, habitat complexity, protection from predators, riparian cover and connectivity also important (Supplement 2). Groundwater input was highlighted as an important factor for flow permanence and cooler temperatures (Van Horn et al., 2022), and sites with more groundwater input may serve as refugia because of greater decoupling from local climate conditions (Beatty et al., 2010; Hopper et al., 2020).

3 | DROUGHT REFUGE IDENTIFICATION

Our understanding of drought refuges and the best methods for identification are limited with few studies that explicitly focused on identifying drought refuges for fish (but see Vander Vorste et al., 2020; Yu, Rose, et al., 2022). Most studies focused on physical delineation of surface water presence with limited consideration of biological quality. We see refuge identification as a multi-step process and build on thermal refuge identification approaches (Isaak et al., 2015) to propose a framework that, while written in the context of drought, can apply to identifying refuges (or refugia) from numerous disturbances (Figure 3).

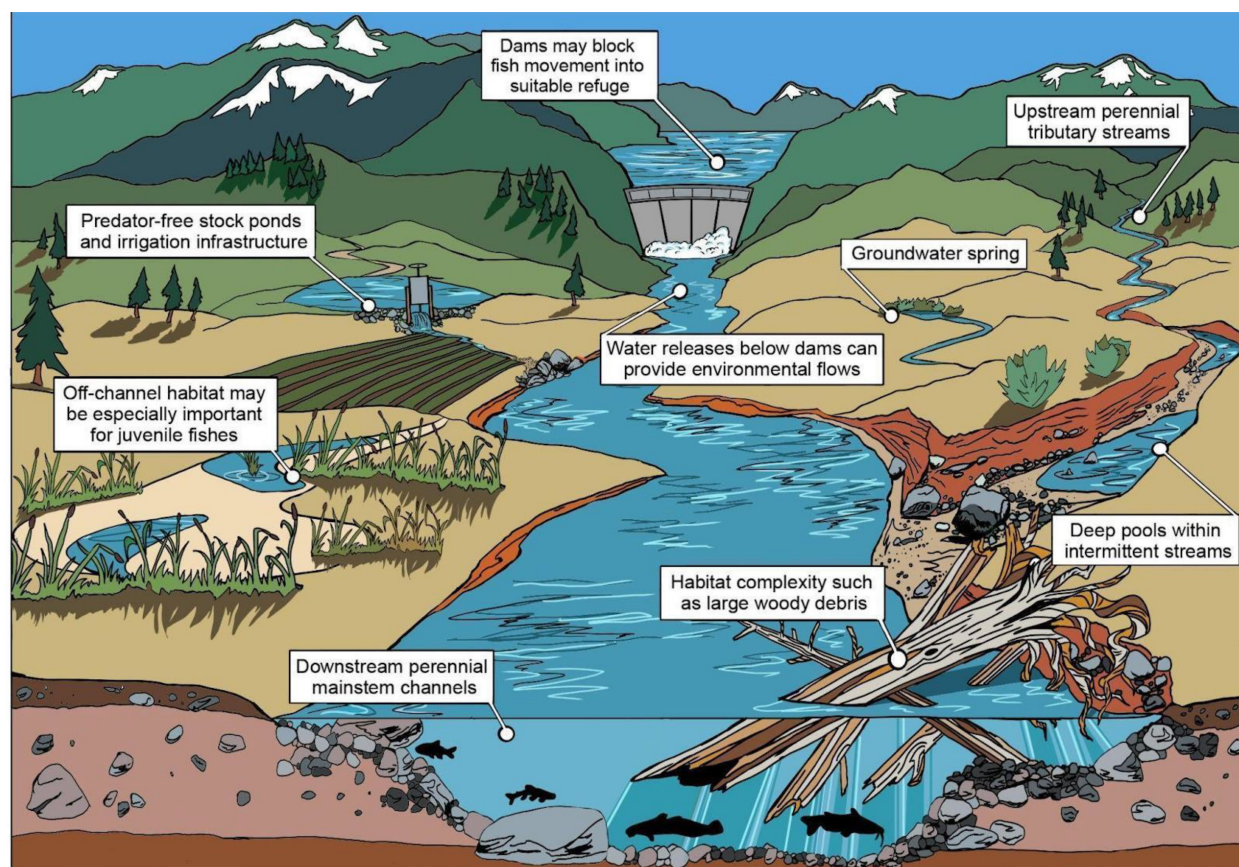


FIGURE 2 Potential fish drought refuges across the riverscape. Graphic by Benjamin Regan.

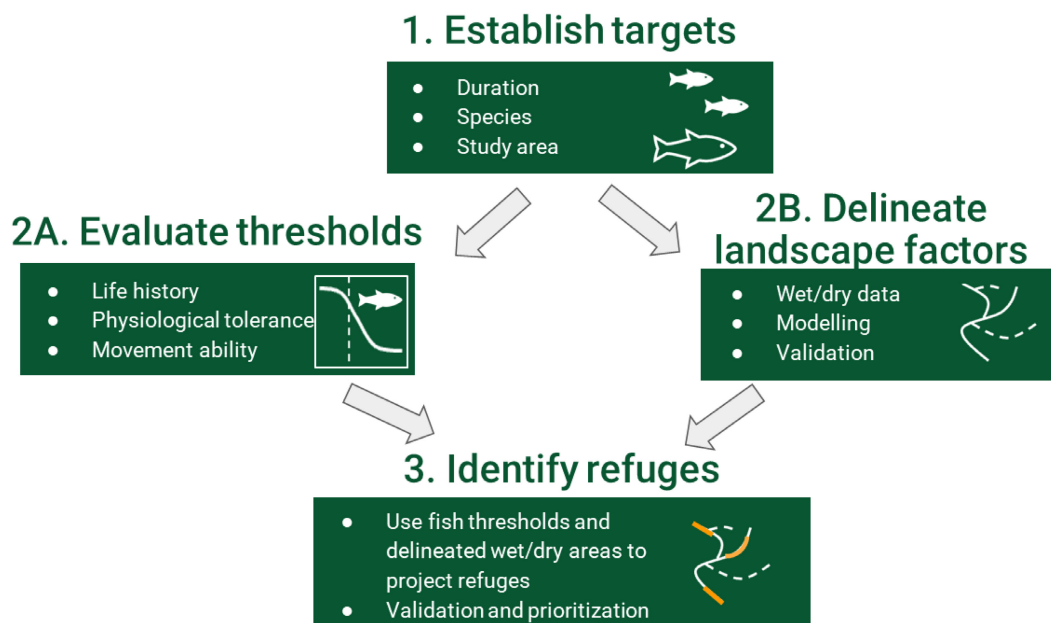


FIGURE 3 Drought refuge identification framework. The framework can be altered to address refuge identification across species and taxa.

3.1 | Standardized framework for drought refuge identification

Step 1. Establish targets—determine the study area, target species/life-stages and required duration of the refuge.

Step 2A. Evaluate thresholds—for the target species, determine the minimum thresholds for population persistence for the desired duration of time. These thresholds can be both abiotic (e.g. physical size of the refuge, dissolved-oxygen content) and biotic (e.g. minimum population for long-term genetic viability, absence of predatory species).

Step 2B. Delineate landscape factors—map key attributes such as water presence, dissolved-oxygen content or distribution of predator species.

Step 3. Identify and validate refuges—apply the minimum thresholds for fish persistence to mapped/modelled data to determine where conditions are met across the study area. This step also includes subsequent validation and management to ensure refuges are effective.

Although not formally codified, previous thermal refuge studies have completed these steps with success. For example, to determine where thermally sensitive bull trout (*Salvelinus confluentus*) are likely to persist in the face of stream warming, Isaak et al. (2015) established a relevant **target** of population persistence into the 2080s, determined the temperature **threshold** that will allow multidecadal persistence, **delineated** riverscape-level stream temperatures (i.e. NorWeST stream temperature model) and **identified** where these conditions were met by modelling future stream temperatures and species' distributions. Here, we address components of this framework in more detail with application to drought.

3.2 | Step 1: Establish targets

Selection of the target species, study area or spatial scale, and study duration or temporal scale sets the context for subsequent steps. In some cases, the target species is clear due to its status as a species of conservation concern or an economically or ecologically important species. In other cases, it can be challenging, as the species with the best data may not be those with the most need or there may be multiple species of concern. Determining the spatial and temporal scales will vary depending on the nature of the drought event and the ecological needs of the target species. For example, drought duration has substantial implications for the refuge; microhabitat can be important for short-term (days to weeks) persistence, but larger reaches or stream segments are needed to persist through a multi-year drought (Magoulick & Kobza, 2003). Setting spatial boundaries may also be challenging; refuges are often thought of as spatially isolated areas, such as pools within a drying stream, but perennial, mainstem or downstream reaches were also frequently identified in the literature review (18% of studies), and in that case, there is no clear downstream boundary. Instead the study area may be defined as the area for which drought is a concern or the distributional range of the target species. Temporal boundaries are also difficult to define and closely intertwined with spatial boundaries depending on, for example, variability in expansion and contraction of surface water availability throughout the river network and the rate of drying for specific events (Costigan et al., 2016; Malish et al., 2023; Price et al., 2021). However, temporal targets may be guided by hydrologic characterization such as observed recurrence intervals or typical duration of events (McMahon & Finlayson, 2003) although any classification is unlikely to be static given the increasing occurrence

of multi-year droughts and strong carryover effects (Hammond et al., 2022; Lennox et al., 2019).

3.3 | Step 2A: Determine thresholds

Fish drought thresholds will vary with required refuge scale for maintaining viable population sizes, but also the life-history, physiological and behavioural limitations of the target species. Matching the spatial scale of refuges to species distribution and behaviours is important, as not all species will benefit from small, localized refuges (Hale et al., 2018). Movement ability will also determine a species' ability to disperse and recolonize following drying events (Perry & Bond, 2009) and can help guide the needed spatial scale and configuration of refuges on the landscape. For example, larger, more mobile fish may be able to persist in fewer large refuges spaced further apart while smaller fish with reduced home ranges and dispersal abilities may need numerous smaller refuges in close proximity. However, species may be subject to ecological traps if they are not habitat selective or refuge conditions deteriorate (Archdeacon et al., 2024; Hale et al., 2018; Vander Vorste et al., 2020).

An understanding of the physiological or life-history traits of target species can help set thresholds to guide refuge classification and determine if populations of a given species can survive drought conditions relatively unchanged, recover following drought despite negative effects or both (Crook et al., 2010). For example, species with broad physiological tolerances to temperature and dissolved oxygen may only show minor responses when confined to areas of reduced water quality while the same conditions for other species with narrow tolerances may result in mortality (Lennox et al., 2019). Life-history traits are also important. Small-bodied, short-lived fishes that reach maturity at an early age (i.e. opportunistic species sensu Winemiller and Rose 1992) are thought to be less susceptible to seasonal drought because populations can recover quickly after flows resume, and some exhibit continuous recruitment even when restricted to isolated pools (Kerezszy et al., 2011). These opportunistic species tend to be good indicators of streams that are regularly intermittent (Magoulick et al., 2021; Mims & Olden, 2012). Traits that are successful for short-term or seasonal droughts may differ from traits needed to be successful in prolonged, multi-year droughts. Opportunistic species may miss the opportunity for successful recruitment before they die (Chessman, 2013) and may experience population declines despite the presence of refuges. For example, the specialized pelagic reproductive guild of minnows found in the American Great Plains are highly susceptible to stream fragmentation and require continuous flowing water for eggs and larvae during early developmental stages compared to species with other spawning modes (Dudley & Platania, 2007; Nguyen et al., 2023). Although several studies have explored drought-trait associations, threshold predictions based on these connections have yet to be determined.

Organismal measures of drought tolerance useful for identifying refuges may incorporate critical thresholds of survival for water

presence, temperature and dissolved oxygen, as well as connectivity to potential refuge habitats. For temperature sensitivity, projected stream temperatures can be combined with estimates of a fish's thermal tolerance and dispersal ability to identify refuges (Troia et al., 2019). A similar approach could be applied for other physical factors such as water presence. Incorporating connectivity could use metrics such as number of zero flow days (Perkin et al., 2015), stream fragmentation thresholds (Perkin & Gido, 2011), distance to nearest refuge or a flow-pulse requirement (Yu, Rose, et al., 2022). Interactions, especially the presence of aquatic or terrestrial predators, can diminish the value of a refuge (Kobza et al., 2004) and drought may intensify parasitism and infection rates (Lymbery et al., 2020; Medeiros & Maltchik, 1999). As a result it may also be necessary to include a predator presence threshold.

It may not always be feasible to create species-specific thresholds, in which case the creation of thresholds for 'drought guilds' may be a suitable alternative (Baumgartner et al., 2017). For instance, some species confined to isolated pools maintain abundance relatively unchanged or may even successfully reproduce (Hopper et al., 2020; Kerezszy et al., 2011) and may be considered 'drought tolerant'. In contrast, other species experience low or failed recruitment during intermittent conditions (Durham & Wilde, 2009) and may be considered 'drought intolerant'.

3.4 | Step 2B: Delineate landscape factors

Delineation can occur across multiple biotic and abiotic variables including water temperature, meso-habitat, riparian vegetation and predator presence. Delineation approaches fall into three main categories—field, imagery and modelling. We evaluate advantages and disadvantages of these approaches with a focus on surface water availability, an important variable for drought refuge.

Field approaches include on-the-ground longitudinal mapping of water availability by walking the stream (Bănăduc et al., 2021; Turner & Richter, 2011), sensor deployment to monitor wet-dry status in electrical resistance (Jaeger & Olden, 2012), temperature differences, (Arismendi et al., 2017), and more recently, the use of trail cameras (Kelly & Bruckerhoff, 2024). A major advantage of field approaches is that field crews can simultaneously assess fish use by sampling for water quality and the presence or abundance of fishes (Elliott, 2000; Labbe & Fausch, 2000). A disadvantage is that they are not particularly suitable for large study areas due to prohibitive labour and instrument costs. In some cases, this can be overcome with a community science approach (Allen et al., 2019; Detry et al., 2016).

Imagery approaches are faster and can cover larger areas but can have high initial costs and often require specialized training for data processing. Imagery available to evaluate water presence includes both aerial (Thompson et al., 2021) and satellite approaches (Bishop-Taylor et al., 2017; Hermoso et al., 2013) and may include classification based on spectral reflectance. Satellite approaches are limited to wider river channels with little vegetation canopy. Aerial imagery can sometimes be used in locations with canopy cover; however, if

the spatial resolution is too coarse, smaller streams will be difficult to distinguish from the surrounding landscape.

Modelling approaches to determine water presence include hydrologic models (Wenger et al., 2010) and statistical approaches based on machine learning (Jaeger et al., 2019; Moudi et al., 2021). Model inputs often include physiographic and climatic variables while outputs may include streamflow values, proportion of stream segments with water present or probability of streamflow presence. Many hydrologic models appear to struggle at estimating low/zero flow (Staudinger et al., 2011), posing a substantial challenge on their applicability for drought refuge delineation, while statistical models often fail to reflect the continuing decrease of surface water extent within rivers in the absence of precipitation. Recently, a process-based modelling approach was developed specifically for stream pools connected with shallow groundwater; the outputs of the model include persistence of each stream pool and the overall proportion of the stream segment with water present (Yu, Burrows, et al., 2022). Modelling approaches can be time and cost efficient if data are available.

3.5 | Step 3: Identify and validate refuges

The final step combines the thresholds for fish persistence identified in Step 2A with the mapped/modelled data from Step 2B to identify potential refuges across the study area. Many of the mapped factors may be physical (e.g. water presence, water depth, temperature) mirroring work on thermal refuges, but these may also interact with biological factors. For example, selecting areas with sufficient water volume and depth to limit negative inter- or intraspecific interactions and predation by terrestrial predators. Refuges must occur within the geographic distribution of the target species and have at a minimum seasonal connectivity that allows for movement into the refuges during drought, and dispersal after drought events. Validating drought refuge effectiveness in an adaptive-management framework can ensure refuges are functioning effectively and identify when refuge presence shifts spatially or temporally. For example, large floods have the potential to alter streambed morphology, affecting the number and spatial position of stream pools. These shifts may mean that the drought refuge identification framework is repeated to update locations of refuges.

Validation and subsequent management of identified refuges often focuses on maximizing three attributes: (1) persistence, the length of time a refuge retains water during no-flow events; (2) quality, including water quality, water volume, habitat availability and intact food webs; and (3) connectivity among drought refuges. Existing management mechanisms to protect current drought refuges and ensure their persistence include a suite of habitat restoration and water management tools that reduce water extraction from streams (e.g. water leases, instream-flow reservations, efficient agricultural and urban water use, implementation of environmental flows), promote water retention (e.g. protecting beavers) and maximize use of available water (e.g. use of agricultural return flows, timely release of water from dams; Table 1). Mitigation actions to maintain or improve

the quality of aquatic refuges target not only the water quality in the refuges (e.g. artificial aeration), but also the surrounding environment (e.g. riparian protection, fencing). Connectivity among drought refuges can be enhanced by removing unnecessary barriers/dams in the waterways, installing fish passage at instream barriers or protected flows that allow fish movement.

3.6 | Cases studies of drought refuge identification and management in practice

Each step of the refuge identification framework and associated management can be difficult to complete and context specific as illustrated by the following case studies for a large multi-species system, the Murray–Darling Basin of Australia, and a small single-species system, the middle Rio Grande of the southwestern United States. These case studies did not explicitly implement the proposed framework but illustrate how the principles underlying the framework, for example, an understanding of fish physiological tolerances and life history is necessary for identifying refuges and appropriately targeted management.

Severe, multi-year drought in the Murray–Darling basin of south-eastern Australia endangers many endemic fish species, over half of which are listed as threatened (Lintermans et al., 2014). Because the geographic area is large and on-the-ground surveys are not feasible, expert opinion and scientific literature reviews have served to identify at-risk target species and species traits that promote resistance and resilience (or susceptibility to drought) as well as to identify areas where conservation efforts would be most productive (Crook et al., 2010). More recently, satellite imagery and modelling have been used to delineate waterholes (Marshall et al., 2021; Yu, Burrows, et al., 2022). Management has focused on targeted water deliveries that are able to maintain population segments of endemic fishes (Hammer et al., 2013), contribute base flows to support habitat and connectivity, and mitigate risks from hypoxic conditions (Hladyz et al., 2021). Population monitoring of target species has revealed species-specific responses to environmental flows (Baumgartner et al., 2017; Gilligan et al., 2009), helping to establish targeted water deliveries to improve resistance and resilience of focal species, rather than establishing blanket minimum flow requirements (Ellis et al., 2013; Wallace et al., 2008).

The imperilled Rio Grande Silvery Minnow (*Hybognathus amarus*) is the target of seasonal drought refuge management in the middle Rio Grande as reduced precipitation and snowpack, in conjunction with abstraction of surface water for agriculture, has resulted in significant channel drying during summer and autumn months. The management of the river has severed the surface–groundwater connection, leading to stranding and mortality of fishes in isolated remnant pools that can exceed critical temperature thresholds or dry within a few days (Archdeacon & Reale, 2020; Van Horn et al., 2022). Because Rio Grande Silvery Minnow is restricted to approximately 300 km of river (Bestgen & Platania, 1991), intermittent and flowing segments are monitored daily by ground or drone field

TABLE 1 Example threats to the three attributes of drought refuge: Persistence, quality and connectivity, and associated example mitigation action.

Group	Example threat	Example mitigation action
Persistence	Surface and groundwater extraction for irrigation and other human uses	Strong limits or prohibition on pool pumping and/or groundwater pumping near refuges, protection of springs and groundwater recharge areas, enforcement of illegal pumping, efficient agricultural and urban water use
	Altering streamflow regimes through dam construction	Provision of environmental flows during non-drought years to build resilience and optimize recruitment opportunities and ecosystem processes, timely release of water from dams
Quality	Trampling by feral animal and livestock	Restricting access by livestock
	Clearing of riparian vegetation	Riparian zone management, vegetation replanting, Fencing and revegetation of riparian zones
	Water temperature increase and reduction of dissolved oxygen	Artificial aeration (e.g. bubbler)
	Introduced plants and animals	Conservation stocking of locally extinct native fish species in selected refuges, control introduced plants and animals
Connectivity	Increase in pollutants from urban or agricultural inputs	Provision of minimum flows for dilution
	Barriers in waterways (e.g. levee banks, roads), upstream dam construction.	Remove unnecessary barriers/dams in the waterways, installing fish passage at instream barriers, assisted migration or translocation

surveys to delineate flowing and intermittent areas. Large, perennial refuge areas occur around diversion dams and irrigation infrastructure where leakage, return flows or bypassed water can support several kilometres of Rio Grande Silvery Minnow habitat (Cowley et al., 2007). Rio Grande Silvery Minnow is short-lived and can show a remarkable recovery from drought, increasing three orders of magnitude in abundance over a single spawning season (Yackulic et al., 2022). However, recruitment is strongly tied to spring-runoff; therefore, management of summer and fall drought refuges will not improve resilience to drought if spring recruitment remains low (Archdeacon et al., 2020).

4 | MANAGEMENT CHALLENGES AND OPPORTUNITIES

These case studies illustrate how managing drought refuges to promote fish resistance is challenging. Sustained multi-year droughts, complex water policies and lack of water for conservation hinder deliveries of environmental water to refuge areas and limit improvements to drought resistance (Collof & Pittock, 2019; Hammer et al., 2013; Wineland et al., 2022). With continued climate change, it is also likely that the prevalence of drought refuges across the landscape will decrease and locations of viable refuges will shift.

An additional challenge is therefore identifying locations that can serve as refuges now and under a range of future climate change and water use scenarios. This may especially be the case with anthropogenic drought as fishes may lack evolved adaptive behaviours in systems not historically subjected to streamflow intermittency (Datry et al., 2023).

The creation of refuge habitat is one climate-adaptation planning opportunity. Restoration approaches, such as beaver translocation, or the construction of water-holding structures, such as beaver dam analogs, bendway weirs or Zeedyk structures, can increase water storage and create refuge habitat on the landscape (Figure 4; Kinzli & Myrick, 2009; Skidmore & Wheaton, 2022). The creation and use of anthropogenic refuges, such as irrigation canals or water impoundments behind small dams or using treated effluent to augment or create habitat in arid regions, has strong potential to provide water for fish at critical time periods (Halliday et al., 2015; Hamdhani et al., 2020). In Cambodia, community fish refuges—constructed community-managed ponds established in seasonally inundated rice fields—are a government recognized conservation measure to stabilize fish populations by providing safe refuges during the dry season (Phala et al., 2018; Tilley et al., 2024). The acquisition and proactive management of instream-flow rights or water leases and installation of more water-efficient infrastructure can also be used to benefit fishes in drought-stricken systems. Targeted delivery of



FIGURE 4 Management techniques for maintaining or creating drought refuges: (a) Instream flow reservations give governmental agencies water rights to maintain base flows and active monitoring can allow for timely calls for headgate management. (b) Irrigation return flows (entering from left in picture) can be used to strategically create refuge pools. (c) Artificially constructed habitats, such as this Australian farm pond, mimic natural habitats of imperilled species, establishing new populations. (d) Beaver-dam analogs and other low-tech restoration techniques, such as Zeedyk structures, can create refuge pools. (e) Increasing water-use efficiency by replacing flood irrigation with more efficient systems can leave more water for instream flows. (f) Structures, such as bendway weirs, j-hook vanes or root wads, can create scour pools that may serve as refuge during low flows. Image credits: (b) Quantina Martine, Audubon Southwest, (c) US Fish & Wildlife Service, (d) Dominique Shore, Utah State University, (e) Lori Iverson, US Fish & Wildlife Service.

small flows to support drought refuges may increase resilience for sedentary species (Maceda-Veiga, 2013) or species that can recruit during low flows or intermittent periods (Baumgartner et al., 2017; Kerecsy et al., 2011). During severe droughts, lack of water for environmental flows may necessitate rescue efforts for fish species to maintain viable populations (e.g. Lintermans et al., 2014). In increasingly drought-prone systems, long-term management may include translocations and supplementation with hatchery fish (Crook et al., 2010; Ellis et al., 2013; Osborne et al., 2024).

Refuges are often focused on resistance, but shifting to managing for resilience may be another opportunity (Selwood et al., 2019). Protecting aquatic habitats with diverse environmental characteristics may be a strategy for preserving access to refuge sites across years (Schindler et al., 2015). Similarly, connectivity among refuges is critical to allow dispersal, colonization and reestablishment of fishes after a drought (Marshall et al., 2021). When creating or enhancing refuges, the spatial distribution could be optimized to create a 'string of pearls' (i.e. multiple refuges in close proximity) conservation approach (Landis, 2012). Opportunities also exist to build conservation water stores and improve irrigation infrastructure to support

continuous flows (Hatch & Ward, 2023; Veihl, 2023), but implementation and cooperation across management units will be necessary (Crook et al., 2010). Further, across systems, environmental water may further improve resilience to drought if flows match the life-history characteristics of target species (Maceda-Veiga, 2013). A portfolio of actions with environmental water may be needed to support target species at different times of year (Watts et al., 2022).

5 | CONCLUSIONS

Climate change is exacerbating critical water shortages that have intensified due to increasing human water abstraction and use. Knowing the environmental characteristics of refuges that may either contribute to species survival or act as ecological traps are crucial for identifying viable refuges and limits ineffective use of limited resources (Costelloe & Russell, 2014). We describe a framework for drought refuge identification that moves beyond simple surface water delineation to explicitly incorporate fish requirements to create more robust and useful products for management. Field

validation with independent data of refuge use and persistence of fishes through drought will be critical to allow long-term evaluations on effectiveness for improving fish populations (Barrows et al., 2020).

While management of drought refuges is one important climate adaptation tool, water availability may not be the only factor limiting fish persistence, especially for threatened and endangered species that are experiencing multiple stressors. The refuge identification framework proposed here is transferable to the identification of refuges for other stressors and can be used to scale up to long-term refugia identification. The protection, creation and evaluation of drought refuges is one component of a portfolio of climate adaptation strategies for fishes and other aquatic species.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Empirical data were not used for this research. All papers included in the literature review are listed in Supplement 2.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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