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REVIEWS

Toward a better understanding of freshwater fish responses to an increasingly drought-stricken world

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Abstract Drought is a constant and important consequence of natural climatic processes and most freshwater fishes have adaptations to counter its effects. However, a changing global climate coupled with increasing human demand for water is reducing the availability of fresh water to fishes and contributing to more frequent and intense drought around the globe. A clear understanding of how fishes, fish habitat, and fisheries are affected by extended drought is needed to help resolve conflicts over water. We therefore identify key questions and research themes to promote the conservation of freshwater fishes as drought increases in length, frequency and severity. (1) How does drought affect fish habitat? (2) What is drought tolerance in fishes? (3) What are drought refuges for fishes? (4) What kills fish during drought? (5) What is the nature of species succession in drought-stricken waters? (6) What are the long-term consequences of drought to fishes? (7) How does climate change affect drought-fish interactions? (8) How does drought influence fisheries? Our limited ability to provide answers to these questions indicates that fish diversity and abundance worldwide is threatened by drought. Planning, including collection of long-term data, is necessary so that conservation and water re-allocation strategies can be implemented in a timely manner to maintain habitats necessary to support biodiversity during drought periods. Without increased understanding of physiological and behavioural factors that determine the tolerance of fishes to drought, it will not be possible to establish realistic targets for management and restoration of populations and species confronting increasing drought frequency and severity.

Keywords Abstraction · Climate change · Disturbance · Fisheries · Flow regulation · Hydrology

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Introduction

Droughts are natural features of the hydrological cycle that create opportunities for healthy succession within freshwater and estuarine communities (Vörösmarty et al. 2010; Xenopoulos et al. 2005; Dai 2013). Droughts can also be viewed as natural disasters with extreme ramifications for society and the environment (Mishra and Singh 2010). Indeed, droughts are perhaps the most economically devastating of natural disasters, with costs exceeding those of earthquakes and many hurricanes because they affect large regions often for prolonged periods (Ross and Lott 2003; Cook et al. 2007; Mishra and Singh 2010). Although droughts reflect natural variation in the hydrological cycle, their effects are becoming more severe as water becomes increasingly scarce because of human-mediated alterations to the hydrosphere (Vörösmarty et al. 2010; Dai 2013). Frequency, severity, and duration of droughts are being increased by human activities. The most significant of these activities include those that accelerate climate change and those that extract water from streams, lakes, and aquifers for agricultural, industrial, and domestic use (Bond et al. 2008; Dai 2013; Langerwisch et al. 2013; Trenberth et al. 2014). More subtly, altered freshwater discharges into estuaries and coastal seas affect habitats where marine fish self-medicate from marine pathogens (Halttunen et al. 2018), find thermal refuge (Poulakis et al. 2011), or grow before returning to spawn in the marine environment (Miller 2016). These changes affect far more than just freshwater systems because reduced flows to estuaries and coastal waters can cause major ecosystem changes and reduced connectivity between freshwater and marine environments (e.g. Zampatti et al. 2010; Crook et al. 2015).

The increasing attention paid to drought is associated with their devastating consequences (Table 1) as global climate change enhances drought (Mishra and Singh 2010). Temperatures have progressively warmed through the late 20th and 21st centuries and are projected to continue increasing (IPCC 2007), accelerating evaporative water loss and contributing to drought (Gregory et al. 1997; Dai 2013; Trenberth et al. 2014). Simultaneously, patterns of atmospheric and oceanic circulation and precipitation are shifting (Dore 2005; Kim et al. 2014). Increased frequency (but see Sheffield and Wood 2008 who argue that extremes, but not means, will be most affected) and severity of natural drought is therefore anticipated globally (Xenopoulos et al. 2005; Mishra and Singh 2010; Dai 2013; Langerwisch et al. 2013; Diffenbaugh et al. 2015). Overall, a trend towards a more variable climate including altered drought dynamics will be exacerbated by continued growth in human populations and associated demands for fresh water, resulting in anthropogenic droughts (Xenopoulos et al. 2005; Mishra and Singh 2010; Kelley et al. 2015). The combined effects of climate change and increasing water use are causing fundamental changes to key components of aquatic ecosystems (see Baron et al. 2002). When there is a conflict between protecting ecosystems and providing water for people (e.g. Falkenmark and Rockström 2004), the requirements of people are generally given the highest priority. Therefore, there is a need to understand how drought affects aquatic ecosystems and biodiversity to identify strategies to minimize damage or to offset loss of ecosystem services, whilst also meeting human demands for water (Mishra and Singh 2010).

Fishes are often the most conspicuous, best studied, and most highly exploited component of aquatic ecosystems, and so are appropriate to use to generate an understanding of drought impacts (Helfman et al. 2009). Fishes tend to exhibit rapid and easily measurable changes to physiology or demography in response to the environment and are therefore early indicators of ecosystem health (e.g. Chapman et al. 2015; Jeffrey et al. 2015; Lennox et al. 2018a). Moreover, fishes range from primary consumers to apex predators and are critical to nutrient cycling and material and process subsidies (Polis et al. 1997; Holmlund and Hammer 1999). Fish can be highly mobile, even in small streams (Gowan et al. 1994), and many species exhibit regular movements both within and among aquatic systems to exploit spatially and temporally discrete habitats of variable productivity (Harden Jones 1968; Lucas and Baras 2001). The reliance of freshwater fish populations on habitat connectivity is pivotal to their long-term sustainability (Jackson et al. 2001; Amoros and Bornette 2002; Branco et al. 2012), rendering fishes particularly susceptible to the effects of drought (Larimore et al. 1959; Lake 2003). Given the myriad ecosystem services provided by freshwater fishes (Holmlund and Hammer 1999; Lynch et al. 2016), drought-mediated alterations to fish populations have the potential to affect not just aquatic ecosystems, but also livelihoods and food security (Wilhite and Svoboda 2000; Epstein and Defilippo 2001; Cooke et al. 2018).

There are increasingly high-profile examples of drought influencing fish and fisheries around the globe (Table 1) and the extent and severity of drought are widely projected to increase (Dai 2013; Guerreiro et al. 2018). Despite growing realization of the negative effects of drought on freshwater fishes, a review of impacts of drought on fishes is lacking.

Table 1 Select headlines from around the world pertaining to fish and drought in 2015. Articles were searched using the Lexis-Nexis database and selected for relevance and geographical diversity

Article title	Date	Publication	Jurisdiction
Fish valued at N$6 million for drought relief	17/12/2015	New Era	Namibia
Drought prompts fishing restrictions in area rivers	18/07/2015	Skagit Valley Herald	Skagit Valley, Washington State, USA
Drought spawns fish fears	06/10/2015	The Phnom Penh Post	Cambodia
Salmon returning, but drought concerns persist	21/11/2015	The Record	Stockton, California, USA
Concern for fish in lake as drought goes on	30/11/2015	The Examiner Newspaper	Tasmania, Australia
Worsening drought bans freshwater angling; may put spawning in jeopardy in Island rivers	07/07/2015	Nanaimo Daily News	Nanaimo, British Columbia, Canada
Drought puts western fisheries in hot water: Near-lethal conditions found in 54 rivers	12/07/2015	Spokesman Review	Spokane, Washington, USA
Lingering drought heightens worries of extinction for salmon	29/10/2015	Monterey County Herald	Monterey, California, USA
Parched State—Fishermen in drought-hit Marathwada in trouble too	13/09/2015	Times of India	India
Mission to salvage fish stocks from heat divides lake	23/12/2015	The Weekly Times	Australia
10,000 fish rescued from low rivers	23/02/2015	The Timaru Herald	Timaru, New Zealand
Trout streams flow again as rain returns	10/04/2015	Canberra Times	Canberra, Australia
Lachlan fish to reap benefits of environmental watering	06/08/2015	Cowra Guardian	Cowra, Australia
Drought laying waste to crops, animals are dying; One farmer pumping water into a dam to try to save the fish that are left	16/11/2015	The Star	South Africa

There are many lingering questions regarding the behavioural and physiological responses of fish to drought, and associated demographic processes, across different habitat types and geographic regions (Humphries and Baldwin 2003; Lake 2003, 2011; See Fig. 1). In this review, we examine consequences of drought for fishes. From a fish perspective, natural droughts can be (1) *seasonal droughts* that occur predictably on an annual basis for short intervals, (2) *multi-year droughts* that re-occur at irregular intervals, and (3) *long-term droughts,* infrequent but prolonged droughts lasting 10 or more years. The changes wrought by more severe and prolonged droughts to aquatic ecosystems require a new management paradigm, reflected by improved management of fishes, fish habitat, and fisheries. We discuss the existing literature and identify knowledge required to address emerging uncertainties. Our aim is to summarise key problems that policy makers need to consider in dealing with drought and to identify priority responses for dealing with the problems, from the perspective of ecological requirements of fishes. Specifically, we address the following questions:

1. How does drought affect fish habitat?
2. What is drought tolerance in fishes?
3. What are drought refuges for fishes?
4. What kills fish during droughts?
5. What is the nature of species succession in drought-stricken waters?

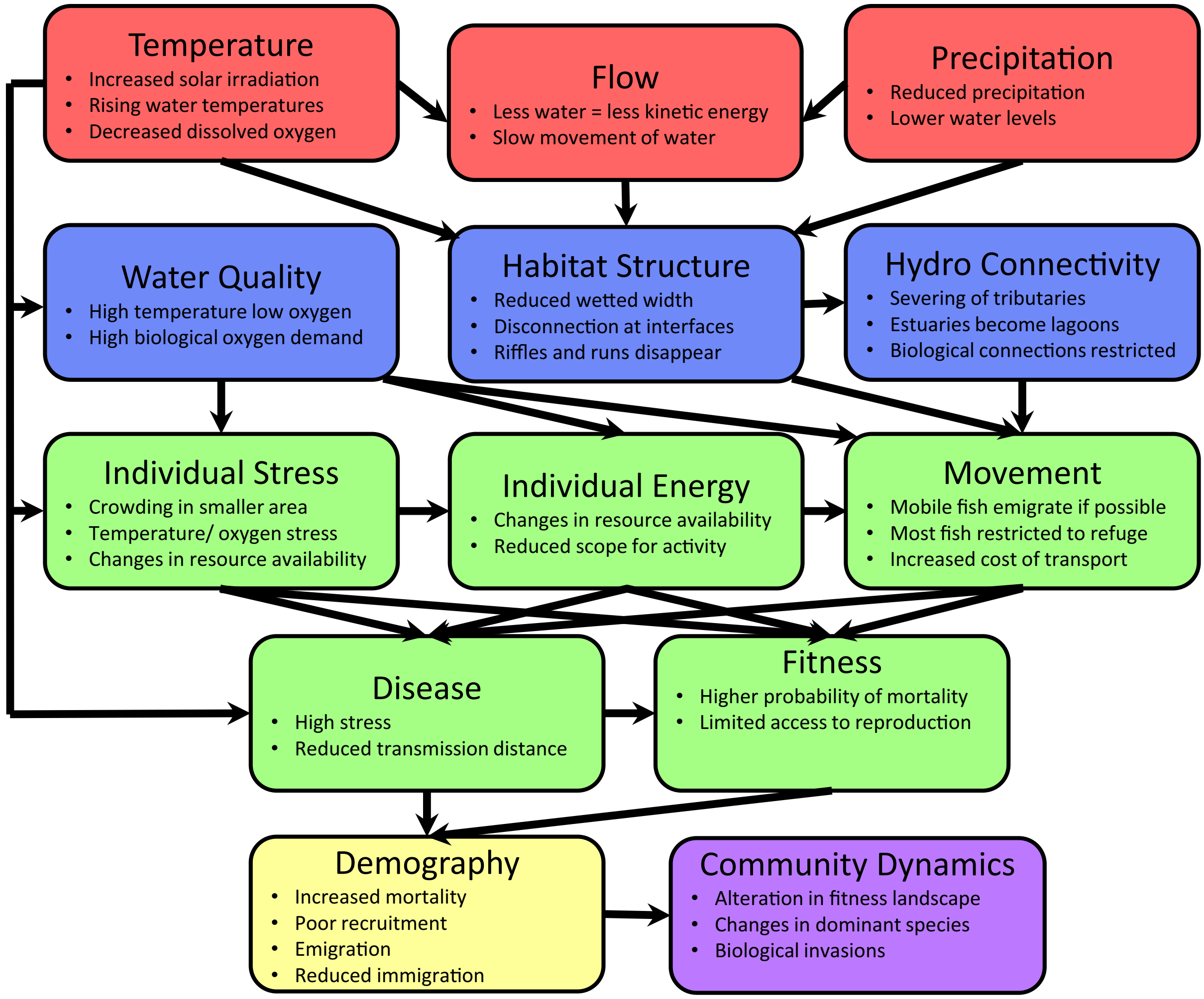

Fig. 1 Network of changes associated with drought in aquatic systems at the phyischochemical (red), habitat (blue), individual animal (green), population (yellow) and community (purple) scales. Changes to temperature and precipitation contribute to low flows, which shift the energy dynamics within aquatic systems, alter habitat features and lateral and longitudinal connectivity, which can ultimately chnage the survival, reproduction, and persistence of fish in aquatic systems. In this paper we review literature to develop an understanding of the role of key nodes in this network and important knowledge where a poor understanding of the abiotic and biotic processes underlying drought constrains the ability to manage fish and fisheries in drought

6. What are the long-term consequences of drought to fishes?
7. How does climate change affect drought-fish interactions?
8. How does drought influence fisheries?

How does drought affect fish habitat?

Species diversity in fresh water is influenced by site characteristics (Vannote et al. 1980; Xenopoulos and Lodge 2006). According to the river continuum concept (Vannote et al. 1980), larger river systems have a higher proportion of autochthonous production, supporting a greater diversity of species. In some systems, this productivity can be exported to downstream waters including estuaries, a process that is attenuated by drought (Dolbeth et al. 2008). Higher flows tend to increase productivity in river systems by increasing available habitat for ecological processes, especially by inundating floodplains and riparian forests (Opperman et al. 2017). In addition, discharge into estuaries connects discrete habitats and creates productive habitat for estuarine specialists (Whitfield 1990; Dolbeth et al. 2008). Drought, in contrast, may limit the biological potential of aquatic systems (Junk et al. 1989; Thorp and Delong 1994; Guégan et al. 1998). Streams that receive less precipitation and glacial melt water are more vulnerable to water loss and may desiccate, although spring-fed lotic systems usually retain flow through low rainfall periods and are especially resistant to desiccation (Lusardi et al. 2016). Habitats that contain large volumes of water (e.g., deep pools in large rivers, large lakes) are also more resistant to desiccation (Castello 2008; White et al. 2016), which can result in persistence of the fish assemblages in such areas except in the most extreme droughts (Love et al. 2008). Likewise, lakes are typically more resistant to drought and provide limited refuge to stream fishes that become displaced.

Drought may reduce habitat complexity in fluvial systems by eliminating riffles, disconnecting pools, and desiccating long reaches of stream (Elliott 2000; Hakala and Hartman 2004). In coastal stream mouths, lagoons are liable to form during drought via the formation of sand bars, severing connectivity to marine habitats (Tramer 1977; Attrill and Power 2000; Bucater et al. 2013). Tributaries (including lateral floodplains) provide an important source of organic matter into mainstem rivers, which functions to drive food webs and other ecological processes. By reducing the flux of organic matter, drought can have drastic effects on carbon dynamics in rivers (Conallin et al. 2011; King et al. 2012). For example, in the Murray River in Australia, a large pulse of organic matter from the floodplain to the main channel during floods following rewetting of a drought-stricken floodplain resulted in high biochemical oxygen demand and anoxia that caused fish kills along more than 1000 km of river (King et al. 2012).

In tropical dry seasons, fish distributions become restricted as some habitats (e.g. flooded forests) disappear (Galacatos et al. 2004). Remnant floodplain lagoons in the Brazilian Pantanal were prone to desiccation and fish kills during drought years (Arantes et al. 2013). In wetter years, these same lagoons provide spawning habitat for important species such as arapaima (*Arapaima gigas*). Extreme drought in the Amazon can sever connections to floodplains creating hyperstability (a phenomenon in which high catch rates are sustained despite decreasing abundance; Pinaya et al. 2016) and was shown to have instigated a shift in the fish assemblage favouring primary consumers; these changes persisted even after drought conditions ameliorated (Röpke et al. 2017). In temperate regions, meltwater from snow that normally inundates streams can be missing in droughts; this causes the ice to break up via thermal deterioration (Prowse and Beltaos 2002); the ice can then erode banks and scour substrate, destroying eggs/nests or killing fish (Scrimgeour et al. 1994). Water quality in streams also declines as the remaining water heats faster and deoxygenates more rapidly with a smaller volume and less mixing. In estuaries, the water may become more saline, shifting the fish assemblage away from freshwater species to more marine species (Parker 1955; Attrill et al. 1996; Wedderburn et al. 2012). For example, Steichen and Quigg (2018) observed contracted distribution of stenohaline blue catfish (*Ictalurus furcatus*) under drought compared to other euryhaline estuarine species.

Lake water recedes during drought, exposing nearshore habitat and eliminating margins that provide essential habitat for many littoral species, such as downed trees and other large wood (Gaeta et al. 2014). In natural lake systems, fish may emigrate from inflowing and outflowing tributaries into lacustrine habitat during drought, but little is known about how fish within a basin alter habitat use in response to drought beyond moving into deeper water. Reservoirs, especially those used for water supply, typically fluctuate very differently from lakes because they are subject to continuous manipulation. Many reservoirs are annually drawn down, simulating seasonal drought effects; during long-term droughts they may dry completely or become lowered to a minimum stagnant pool. Paller (1997) evaluated the fish assemblage in a drawn-down reservoir and observed a 50% reduction in volume and surface area that altered fish abundance and community structure until the original water level was restored 3.5 years later. Low water in winter can increase the risk of anoxia and winterkill (Sullivan 1986; McGowan et al. 2005; Cott et al. 2008), which may be major limiting factors for fish although this is not well documented from a drought perspective.

Drought affects fish habitat in diverse ways, depending on the class of drought, the system, the aquatic community, and the season. Larger river systems are generally more drought-tolerant than smaller systems. Despite longitudinal differences in habitats within the rivers, marginal habitats may disappear, lotic areas may become lentic, and connectivity may be reduced or eliminated. Seasonal impacts of drought require more investigation, particularly if seasonal droughts become prolonged. Negative effects of prolonged drought on fish movements, including migrations, may require long intervals for recovery, yielding persistent changes in fish assemblages because of habitat loss during drought (e.g. Röpke et al. 2017).

Overall, the effects of drought on habitat are as diverse as the habitats themselves. In general, fish habitats become reduced in size and diversity, so extended droughts, especially when aggravated by dams and diversions, may cause permanent changes in the fish fauna. However, the ability of 'natural' assemblages of fishes to return to a post-drought stream or other waters, depends on the availability of refuges and the degree to which the flow has been altered from the historic regime.

What is drought tolerance in fishes?

Drought imposes abiotic and biotic environmental conditions upon fish with consequences for physiological functioning; shifts in magnitude and variation of temperature, flow, oxygen, turbidity, salinity, conspecific density, and other stressors can all yield a stress response (see Whitney et al. 2016a for a review of climate change impacts on fish physiological functioning). Generally, species are considered tolerant or intolerant when confronted by stressors, with tolerance considered to be an evolutionary trait responding to variation in environmental quality. Mechanisms of tolerance include resistance (e.g. physiological tolerance) and resilience (i.e. the ability to adjust to change through behavioural or physiological mechanisms; Ross et al. 1985). Broad physiological scope (tolerance of low dissolved oxygen, high temperatures, etc.; Crook et al. 2010; Chessman 2013), large body size, high fecundity, and vagility are traits permitting individuals to locate refuges such as permanent springs and deep pools (Chessman 2013; Crook et al. 2010). Resilience may manifest as increased reproductive rates or vagility as adaptive responses to cope with drought (Connell and Sousa 1983; Dexter et al. 2014). Brown trout (*Salmo trutta*) exhibit resilience by avoiding seasonal drought when they disperse to brackish or salt water (Klemetsen et al. 2003) and some may spawn in estuaries if necessary (Limburg et al. 2001). In central California, droughts can abbreviate or eliminate annual inundation of floodplains and force floodplain dependent fishes to shift spawning and rearing to marginal habitats (Moyle et al. 2007; Opperman et al. 2017).

Life history traits conferring drought resistance can be highly diverse and context-dependent. Opportunistic spawning to capitalize on favourable conditions is a resilient trait (Olden and Kennard 2010), but the success of species with this trait depends on the class or duration of the drought and the size of the system. In Amazonian floodplains, planktivores, herbivores, and detritivores increased during drought at the expense of carnivores and omnivores, but species diversity increased in years following drought (Freitas et al. 2013). Röpke et al. (2017) studied succession through an extreme drought year (2005) and found that changes in the fish assemblage persisted following the drought, with higher trophic level fishes found at lower abundance. Native fish faunas of Mediterranean-type climates and arid regions exhibit strong drought tolerance because they experience hot, dry summers during which stream flows either cease or drop to low levels annually (Ingram and Malamud-Roam 2013; González-Ortegón et al. 2015; Whiterod et al. 2015). Fish faunas of such regions tend to be species-poor but tolerant to droughts and capable of rapidly recolonizing formerly dry habitat after the drought ceased (Moyle 2002). Moyle (2002) proposed that the morphological diversity among native Californian fishes is the result of strong selection pressures during long-term droughts; fish that survived best in remnant habitats were species experiencing reduced competition for limited resources, driving selection for divergent traits and niche partitioning.

Biological invasions have provided some opportunities to compare the tolerance of native species to aliens. Native fishes may be naturally adapted to drought resistance through long life spans (7–10 years or more) or high fecundities (Moyle 2002), allowing delayed reproduction and rapid recolonization (Kiernan and Moyle 2012; Mount et al. 2017). Non-native species, in contrast, may lack such adaptations so decline from drought effects. Thus, Closs and Lake (1996) showed that drought in an Australian stream caused high mortality of introduced brown trout (*Salmo trutta)* providing an advantage for the native galaxiid *Galaxias olidus*, which was more resistant to low flows, high water temperatures, and low dissolved oxygen. Native fishes can persist in severe droughts where they have evolved under those conditions (Smith 1982), but novel droughts may challenge many native species. Smith (1982) found that drought eliminated most non-native fishes from a California stream (e.g. bluegill, goldfish, green sunfish) but they were able to recolonize from reservoirs that had residual pools. An eradication program in California simulated the effects of drought by wiping out most native fishes from a river (Moyle et al. 1983). Because a few individuals were missed by the toxicants, within 10 years the river was once again dominated by the native fishes. Because of these adaptations, fishes in California streams and rivers that historically suffered from effects of major droughts could rapidly recover populations when flows returned. This is becoming much more difficult because dams of all sizes both divert water and block movement of fishes needed for recolonization (Moyle 2002; Radinger et al. 2018). In other parts of the world, some species of fish are capable of surviving for extended periods in the absence of surface water by aestivating in sub-surface burrows in moist substrates, but such adaptations are rare and highly specialized (Pusey 1989; Ogston et al. 2016).

Drought tolerance and resistance to invasive species is therefore highly context specific and depends on the traits of native and invasive species. In many instances, alien fishes are favoured by drought conditions. In a tropical Puerto Rican watercourse, for example, alien species abundance was amplified during drought (Ramirez et al. 2018). In an Iberian stream, invasive pumpkinseed (*Lepomis gibbosus*) became abundant during drought and native fishes were released from the competitive exclusion only when drought ceased (Bernardo et al. 2003). In a California stream, establishment and spread of invasive green sunfish (*L. cyanellus*) was attributed to the effects of a 5-year drought (Bêche et al. 2009).

Whereas many fishes may tolerate drought, there still may be costs to persisting through one. Thus, Sammons and Maceina (2009) observed slow growth of riverine redbreast sunfish (*L. auritus)* during dry years. Some species may benefit from drought if competition or predation are relaxed. Orangethroat darter (*Etheostoma spectabile*), for example, exhibited increased growth, condition factor, and fecundity during drought (Marsh-Matthews and Matthews 2010). Likewise, Morrongiello et al. (2011) found that fish growth in Australian lakes declined as water levels dropped during drought years but growth increased in wetter years.

Overall, fish responses to drought can vary greatly among species. Some species are highly adapted to live through severe drought, especially in streams. These adaptations can offer some protection to fishes native to regions where droughts occur on a regular basis, by excluding poorly adapted non-native fishes. Unfortunately, non-native fishes often persist in such habitats anyway, through prior adaptations or taking advantages of refuges provided by people.

What are drought refuges for fishes?

The nature of drought refuges varies among species. As discussed above, species with high physiological tolerances can survive for long periods in remnant pools of water having poor quality. Other species (e.g., most salmonids) may only persist where cold, well-oxygenated water exists, perhaps fed by permanent springs or seeps or remaining in deep pools or stratified lakes. The other option for species is to leave the drought-stricken water and find refuge in larger bodies of water, before connections are lost.

Vagile species predictably emigrate out of susceptible systems to avoid stranding or desiccation but sedentary species may also disperse to find refuge when drought sets in (Perry and Bond 2009; Driver and Hoeinghaus 2016; Mount et al. 2017). Large, deep pools in lotic systems with connections to groundwater are most likely to persist through low water and provide refuge needed for some fish to persist (Power et al. 1999; Hayashi and Rosenberry 2002). Water depth and surface area for wind action can determine the temperature and dissolved oxygen conditions in the refuge via mixing of the surface water (Magoulick and Kozba 2003). Refuges may also be areas near inflows of springs when available (Baker and Jennings 2005) or, in tropical systems, floodplain ponds. *Arapaima gigas*, an air-breather, is found in floodplain ponds that are wetted throughout the dry season and provide refuge from fluctuating conditions of the mainstem river (Castello 2008). In Papua New Guinea, fish moved from drought-exposed lakes to floodplains (Swales et al. 1999), but in the Amazon, suitable connections may disappear and strand fish (Pinaya et al. 2016). Sedentary species that cannot make the necessary movements to find refuge may have alternate strategies such as burrowing (Davey et al. 2006), but many fish die as the availability of suitable water quality in refuges declines during extended droughts.

The timing of emigration to a refuge is normally cued by onset of stressful conditions. Cucherousset et al. (2007) found that the timing of emigration of species from a drying wetland was positively related to indices of physiological tolerance. Fish stranded in remnant water can attempt to burrow into substrate (Davey et al. 2006) but high mortality typically occurs due to hypoxia, thermal stress, predation, or disease (Tramer 1977). Often, the amount of refuge area is insufficient to support the entire population (Baker and Jennings 2005) and there will be increasing competition over time. Driver and Hoeinghaus (2016) found that the distribution of fish species in remnant habitat was non-random. Juvenile brook trout (*Salvelinus fontinalis*), for example, selected areas with suitable physical conditions (temperature, cover) over those with more food available, which was reflected in reduced growth (Sotiropoulos et al. 2006; see also Harvey et al. 2006; Grossman et al. 2010).

Refuges often do not provide the full suite of habitats necessary for individuals to complete their life cycle, particularly spawning habitat (e.g. pelagic spawners; Perkin et al. 2015). White and Rahel (2008) found that in extreme drought, most reproduction of Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) occurred in a natural tributary where suitable conditions for spawning persisted whereas appropriate conditions were completely lost in modified reaches of the stream system. However, Freeman et al. (1988) found that abundances of fishes in an Appalachian stream were unchanged by drought despite reduced spawning habitat, owing to density dependence.

Drought refuges are clearly important to many fishes that would not otherwise persist in drought-stricken streams. The nature of the refuge depends on the fish species and life stage, and persistence of a species may require much more than just permanent water, especially for spawning and rearing of juveniles.

What kills fish during droughts?

Aquatic animals in drought experience both temperature and oxygen stress because of dewatering and become crowded with predators and competitors into smaller areas as habitat disappears. Near marine confluences of rivers, hypersaline lagoons can form from which freshwater species are excluded (Vivier et al. 2010). Refuges must be shared by many aquatic species including both fast-water and slow-water guilds (Boulton and Lake 1992), potentially disfavouring lotic species but allowing their persistence in the short term (Jowett et al. 2005; Freeman and Marcinek 2006). Riffle-dwelling fishes forced into remnant pool habitat may experience high mortality (Avery-Gomm et al. 2014). Species in drought refuges must compete for space and resources and become increasingly exposed to competitors, predators, and diseases. Lowering of water levels and aggregation of species in habitable refuge areas disconnects populations, potentially severing connections to spawning grounds and shifting relative abundances (Vivier et al. 2010). Drought can cause behavioural changes in fish as crowded conditions generate competition and predation. For example, burbot (*Lota lota*) established dominance hierarchies as shelter became limiting, with growth advantages going to individuals that secured preferred shelter (Fischer and Öhl 2005).

The effects of drought on fish assemblages can also have broad consequences for food webs in aquatic ecosystems. For example, Dorn (2008) showed that reductions in fish populations in wetlands during periods of drought resulted in increased abundance of crustaceans and large aquatic insects. Shifts towards species with different trophic characteristics—for example, from predatory fish to detritivorous crayfish—have the potential to drastically alter food web structure under drought conditions (Power et al. 2008). Likewise, aerial and terrestrial predators focus on areas where fish are concentrated, altering food webs by selectively preying on larger fishes, although Tramer (1977) found birds mostly feeding on carcasses of dead fish in desiccating pools rather than preying on the fish directly. Zaret and Rand (1971) observed shifting specializations in fish diets between the dry and wet seasons in Panama, suggesting that species forced together in refuge habitat experience intense resource competition and therefore alter their diets (also Wedderburn et al. 2015).

Concentration in small areas can cause crowding stress in fish (Wedemeyer 1976) and disease transmission has been demonstrated to increase in crowded conditions because of shorter transmission distances (e.g. *Saprolegnia infection*, bacterial fin rot, furunculosis in aquaculture; Pickering and Pottinger 1989). Periods of low flow were associated with peaks in the normal cycle of disease in an intermittent stream in Brazil (Medeiros and Maltchik 1999) but there is a poor overall understanding of the role of disease outbreak and recovery during drought (Crook et al. 2010). Predictions about changes in fish disease are made by Marcogliese (2001), with low flow favouring certain fish parasites such as blackspot disease (*Uvulifer ambloplitis* and others), cataracts (*Diplostomum spathaceum*), and white grub (*Posthodiplostomum minimum*) and resulting in increased blindness of fish and incidence of blackspot disease. However, Mitro (2016) observed that many of the changes associated with pathogens were enhanced (or, perhaps in some circumstances, mitigated) by other stressors such as competition with an invasive species. Given that drought affects species other than fishes, it could be predicted that changes in distribution of migratory birds (e.g. Johnson et al. 2005), disturbance to aquatic snakes (Vogrinc et al. 2018), and reductions in amphibian populations and freshwater invertebrates will alter the intermediary host–pathogen dynamics that drive many disease cycles in fresh water.

Connectivity among habitats is often crucial for persistence of fish assemblages during drought (Hurd et al. 2016). For example, spawning sites become constrained in years of low flow, suggesting that drought will favour fishes that are able to reproduce within drought refugia (Parry et al. 2018). Migratory species, including potamadromous fishes, may be particularly affected by the disconnections forged by drought (Beatty et al. 2014). Tropical species, such as the potamadromous *Arapaima* spp., may have difficulty accessing floodplain ponds where they breed during the dry season or those ponds may desiccate with unknown consequences to their populations (Castello 2008; Lennox et al. 2018b). Ria lakes in the Amazon that remain connected to the main river channel therefore provide refuge to fish communities during extreme drought (Carvalho et al. 2018). Disconnection of rivers by dams or drought can also have negative impacts on the capacity for fishes to tolerate drought as they become unable to shift their habitat use in synchrony with the prevailing environmental challenges (Radinger et al. 2018).

In short, fish assemblages are likely to change as drought progresses and communities are restricted to refuges, under crowded conditions. As conditions deteriorate, species most likely to survive will either be those that can leave before connections are lost or those that have broad physiological tolerances. Mortality of remaining fish is usually the result of predation by birds and mammals (including people), physiological stress, and disease, often all acting at once. Presumably, under severe, long-term droughts, local extirpations of species occur so that fish assemblages in diverse waterways may take a long time to recover to their former structure, if it is possible at all. Succession processes both during and following the drought are therefore important to understand.

What is the nature of species succession in drought-stricken waters?

As flows return following drought, individuals exit refuge areas and recolonize re-wetted areas of the system (Marshall et al. 2016). Depending on the severity of the drought and location of refuges, recolonization of a desiccated stream can be rapid (Smith 1982; Canton et al. 1984; Peterson and Bayley 1993; Adams and Warren 2005). However, repopulation from a small founding population may have genetic consequences when genetic diversity becomes reduced because of bottlenecks (Douglas et al. 2003; Hammer et al. 2013).

Intolerant species (see "How does drought affect fish habitat?" section) and those that have been disconnected from spawning areas may have delayed recovery whereas tolerant species may even have spawned successfully during drought (Garcia et al. 2018). The result is an assemblage that is temporally variable, shifting between tolerant and intolerant taxa as flows fluctuate (Grossman et al. 1990; Gido and Jackson 2010). During a severe drought that dried most of the Pajaro River, riffle sculpin (*Cottus gulosus*) persisted in spring-fed tributaries while prickly sculpin (*C. asper*) survived in pools in the main channel (Smith 1982). The prickly sculpin has high mobility and high fecundity, so within a year they recolonized their former range in the river; the riffle sculpin, with relative immobility, low fecundity, and benthic larvae, recolonized areas very slowly, across multiple years. The legacy of drought can therefore influence species assemblages for many years as succession progresses.

Some species' traits contribute to fast recovery after drought (Marsh-Matthews and Matthews 2010). The most common, generalist species are perhaps the most likely to be early re-colonizers (Whitney et al. 2016b). Increased frequency or intensity of drought can select for tolerant or opportunistic species (Mims and Olden 2012; Stanley et al. 2012), which may drive biotic homogenization (e.g. Elliott 2006). Following drought, fish may rapidly recolonize from refuge or the assemblage may return slowly. Swales et al. (1999) observed a prolonged recovery of the fish assemblages in lakes affected by drought in Papua New Guinea. Species commonness should predict how quickly they return, with more abundant species capable of rapid recolonization. Of course, greater impacts from longer or more severe droughts will prolong recovery and hamper succession. Time lags in recovery must reflect legacies of drought as assemblage members repopulate from remnant populations in years following drought.

Overall, succession of species in drought-susceptible waterways, both during and after a drought, is poorly documented but is an important topic from a conservation perspective, especially if assisted recovery of an assemblage reduced by drought is contemplated. Monitoring how and where species recolonize from is important and may be linked to information about physiological tolerances, swimming performance/movement potential, and habitat preferences. Succession is especially important given that it may take many years for assemblages to recover to pre-drought states (Röpke et al. 2017), with consequences for ecosystem services, fisheries production, and nutrient transfer across interfaces.

What are the long-term consequences of drought to fish assemblages?

Whereas fish assemblages can exhibit remarkable ability to recover following drought, modern challenges can reduce the likelihood of this successfully occurring. Human changes to waterways, climate change, and frequent introductions of alien fish, mammals, invertebrates, and aquatic macrophytes means that droughts are likely to initiate more permanent changes to fish assemblages.

Fish ecologists have long investigated factors influencing the structure of fish assemblages (see, for example, Gido et al. 2010; Ross 2013). Both biotic and abiotic habitat characteristics sculpt each assemblage. The highly variable physicochemical environment in streams suggests that biotic interactions (competition, predation) should be less important than abiotic factors, as evidenced by the relative ease with which stream fish assemblages integrate non-native species (Light and Moyle 2015). Low flow is a stressor to fish (Costa et al. 2017) but the long-term consequences of drought on fish may be variable as stocks fluctuate across years (Freeman et al. 1988).

As water levels lower, temperature, salinity, and oxygen become increasingly limiting so that species intolerant of hyperthermic and hypoxic waters will most likely give way to more tolerant species, yielding an alternative state that is maintained under periodic droughts (Smale and Rabeni 1995) creating new, less diverse assemblages. Frequent, prolonged droughts will likely generate selection for fish species that are tolerant of warm water, low oxygen, and unpredictable food availability and that can skip spawning in unfavourable years. Large fish in some systems are more tolerant of drought owing to their mobility (Matthews et al. 2013), higher fecundity, and lesser physiological demands per unit mass (Kalinin et al. 1993; Bickler and Buck 2007) but they may be more vulnerable to terrestrial predators if they are stranded (McCargo 2004). Their long life also exposes them to risk of premature mortality given extreme drought; therefore, selection imposed by drought must be context specific. Large fish generally decline in catches during drought (Walters and Post 2008; Marsh-Matthews and Matthews 2010; Ferguson et al. 2013; Fabré et al. 2017), suggesting predation and stress indeed selects against the larger individuals, despite traits that should confer tolerance (Sammons and Maceina 2009).

Drought regimes have shaped contemporary fish assemblages. In many locations where there is predictable variability in the flow regime (e.g. seasonal drought), the ichthyofauna is comprised of generalists or opportunists compared to more hydrologically stable streams where fish tend to be specialists (Poff and Allan 1995; Olden and Kennard 2010; Mims and Olden 2012). Interestingly, Matthews and Marsh-Matthews (2003) suggested that drought-intolerant species may already have been extirpated from many watercourses in the midwestern United States, a shifted baseline reflecting the legacy of drought. Kelsch (1994) surveyed the Little Missouri River after a six-year drought and found dominance of three species and an apparent loss of ten species. However, Grossman et al. (1998) observed either stable or increased abundance of fishes in a drought-stricken North Carolina stream. Interestingly, Grossman et al. (2010) observed an increased diversity at upstream sites during drought, attributed to increased accessibility to those sites among flow intolerant species. Ultimately, flow intolerant species proliferate when the flow regime shifts towards a more lentic state (e.g. Gido et al. 2010). With the addition of climate change warming water temperatures, some non-native species may be released to proliferate where they are introduced (Moyle et al. 2013; Light and Moyle 2015).

As drought dynamics shift, fish assemblages respond by shifts in abundance and dominance. In some places, the legacy of drought is already manifested as simplified fish assemblages of tolerant species, including generalists and those with broad physiological tolerance. Permanent changes to fish assemblages are increasingly likely because of climate change and persistent water demand by people as drought and warm water temperatures alter fitness landscapes in fresh water (Bogan and Lytle 2011). In many areas, the changes will be reflected by extinctions of native species and invasions of alien species pre-adapted to the new conditions (Moyle et al. 2013).

How does climate change affect drought-fish interactions?

As we have indicated, climate change is clearly a prominent factor that one way or another will affect persistence of many fishes, with extinctions most likely to occur during prolonged droughts. Increased hydrological variation will be a consequence of warmer global temperatures (Döll and Zhang 2010; Guerreiro et al. 2018), yet little is known about how the prolonged or unpredictable drying of systems will affect the capacity for watercourses to sustain fish diversity and abundance in the long term, nor the broader ecological consequences of changes to fish assemblage composition and abundance. Changes to water levels invariably affect the distribution of habitat within a watershed. Schindler et al. (1996) observed physical and chemical changes to lakes and streams during a period of warming: temperature, clarity, chemistry, and productivity. This study demonstrated the interconnectedness of many physicochemical characteristics of systems and the integrated changes ensuing from environmental stressors. Water levels tend to be highest after seasonal inundation during rainy seasons, from snow-melt flooding, or after intense tropical rainfalls (Smith et al. 1998). Transition to drier or warmer seasons predictably reduces water levels in a cycle that could affect many phenological processes such as reproduction, dispersal, and migration.

Warmer winters yielding less snow and melt water in temperate streams (Knowles et al. 2006) are projected to create flashier, earlier floods or more frequent pulses from rainwater that historically fell as snow. Ultimately, this will yield prolonged, annual, low water and flow through late spring, summer, and autumn. Earlier, flashier floods will alter many of the cues used by fish in their life history (e.g. migration, reproduction, foraging) and be precursors to prolonged annual drought that extends into summer months. In the tropics, Freitas et al. (2013) suggested that the intensity of flood and drought will oscillate more extremely, potentially resulting in species losses in the Amazon. The combined impacts of climate change and water abstraction are projected to significantly threaten the viability of many fish populations, although Xenopoulos et al. (2005) suggested that water conservation could greatly mitigate the damage. Radinger et al. (2018) showed that damming waterways negatively affects species' resilience ability to tolerate environmental disturbance, including drought.

There are many disturbances to local ecosystems anticipated to result from climate change, particularly in terms of temperature and precipitation and therefore water levels and flow. Increased severity and frequency of drought because of global climate change will mean drought is not an isolated stressor, but one that is synergistic with other oncoming climatic changes including flow variability (Costa et al. 2017). Climate change will cause shifts in instream vegetation, riparian species, invertebrate fauna, and predatory mammals/birds that will also have yet unforeseeable consequences for fishes, particularly when coupled with drought (Lake 2003). More research is needed to project where droughts will have the greatest impact and to assess how multiple stressors will operate in conjunction with drought so that actions can be taken to reduce impacts of climate change and drought.

How does drought influence fisheries?

Fresh water supports important commercial, artisanal, and recreational fisheries (Cooke and Cowx 2004; Welcomme et al. 2010; Cooke et al. 2016). Fishers generally target top predators in systems; however, growth of large predatory fish depends on food availability and habitat quality, both of which are strongly affected by drought. Drought stresses fish, constrains their distribution, alters their diets, and can even promote processes such as methylmercury intoxication (Azevedo et al. 2018). Correspondingly, it has been observed that catches in fisheries decline during drought in some systems (Mol et al. 2000; Gillson et al. 2009). In other systems, fishing may concentrate in refuge areas to generate higher catches (Swales et al. 1999; Brookes et al. 2015). Fabré et al. (2016) predicted reductions in Amazonian fisheries yields during periods of high intensity and frequency of droughts while Pinaya et al. (2016) found that river fisheries became more productive as access to floodplain ponds was severed. Similarly, strong negative correlations between low river flows and recruitment, growth, and harvest rates have been reported for barramundi (*Lates calcarifer*) and king threadfin (*Polydactylus macrochir*) fisheries in Northern Australia (Staunton-Smith et al. 2004; Robins et al. 2006; Halliday et al. 2008, 2010). Davies (1978), however, noted that effects of drought were negative on salmonids but positive on warm-water fishes, for which the warmer water temperatures increased feeding activity. Some jurisdictions have regulations governing closures of fisheries during periods of low flow (Porter 1997; Dempson et al. 2001), but the effectiveness and economic impact of such actions are unclear.

Fisheries can have interacting and exacerbating impacts on freshwater fish populations (Ferguson et al. 2010); therefore, close management freshwater fisheries in an era of water scarcity is increasingly important. Precautionary approaches to management are needed to prepare for changes to water levels and to ensure that a diverse portfolio phenotypic and genotypic variation exists to respond to future climatic scenarios (Schindler et al. 2010; Ward et al. 2016). Fisheries management must account for potential dramatic changes in hydrological regimes in affected regions and biological assessments to understand the implications of altered flows on fisheries prodcutivity, and to manage species based on expected adaptations to a drier world (Hammer et al. 2013). Proactive approaches (Crook et al. 2010) and experimental (adaptive) management are necessary to prepare for increased drought frequency in the future (Richter et al. 2006). Given the complexity of water management, such plans will presumably involve several policy and management options or actions related to infrastructure and its operations (e.g., environmental flows), physical habitat alterations (e.g., reshaping channels to provide refuges), riparian restoration, source water protection, among others (see Kundzewicz et al. 2008).

One approach that has been suggested to address the challenge of collecting data for experimental management is using reference waters as indicators of drought. Indeed, the use of indicators and reference points is already common within an ecosystem-based management framework (Jennings 2005; Rogers and Greenway 2005) so using reference waters in drought scenarios should be widely acceptable; it would, however, require identification of relevant mechanistic links and pathways (Lefevre et al. 2017). Although caution must be exercised to ensure reference areas are honest indicators (McCargo and Peterson 2010), Arthington et al. (2006) advocated for reference streams as ecological indicators for physically or ecologically similar systems to inform adaptive management.

Indicator species have been proposed as a tool to inform management during drought (Kanno and Vokoun 2010). Anderson et al. (2006) argued that indicator species should not simply be sportfishes, which would represent an inherently top-down approach, but that instead, such an approach must include diverse members of the local aquatic assemblage. Examples include small species that may be at risk of extinction and species that represent lower trophic levels. The advantage of using sportfishes is that they often have better historical data available and can be used effectively to attract public attention (Ebner et al. 2016). They can therefore be effective indicators if their population dynamics provide relevant information on assemblage responses to drought (Box 1).

Overall, drought has the potential to negatively affect freshwater fisheries, in combination with other changes taking place. Catches might increase as fish become concentrated in the early stages of drought but they will decrease in the long run if habitats are unable to support large enough populations of harvestable fish. Sport and commercial fishes, therefore, have not only high economic value but have special value as indicator species that the public at large can appreciate. Preparing watercourses for drought through proactive conservation and management will be critical to mitigating impacts and sustaining benefits of fish both to fisheries and the ecosystems that they inhabit.

Synthesis

Some key findings of this review are condensed to maxims in Box 2. The synthesis that follows supports these maxims but is more focused on what can be done to reduce the impacts of drought on fish assemblages and populations.

Hydrological extremes are stressors that affect physiological, behavioural, and life history processes in fish (Costa et al. 2017). However, freshwater fishes have evolved in spatially and temporally unstable environments (Douglas et al. 2003; Humphries and Baldwin 2003) and they persist in waters where both seasonal and supra-seasonal droughts are a fixture of the environment (Magoulick and Kozba 2003; McMahon and Finlayson 2003). Indeed, drought is a constant and important feature of the hydrological cycle that emerges periodically and has important ecosystem consequences (Lake 2011). Although fish have evolved to cope with environmental stochasticity, climate change and human demand for fresh water are straining freshwater ecosystems, particularly via damming and water extraction (Postel 1996; Lake

Box 1 Salmonids in California as indicators of drought effects. Inset photograph shows Chinook salmon (*Oncorhynchus tshawytscha*) in a low water stream in their native habitat

California's 10 degrees of latitude encompass a broad diversity of aquatic habitats. Despite its highly variable Mediterranean climate, the state supports 32 species (as defined under the USA's Endangered Species Act) of salmon, trout, and whitefish (Salmoniformes). Most have populations at the southern limit of their distribution; many are endemic and considered iconic. However, most Californian fresh waters have been altered or diverted for human use, so are in a state of perpetual drought. This has resulted in major declines of its salmonid populations, including runs of distinct varieties of valuable Chinook and Coho salmon.

In recent decades, these salmonids have been further stressed by natural drought, notably the 2012–2016 drought, which pushed a number of anadromous populations to record low abundance as habitat deteriorated (Mount et al. 2017). Moyle et al. (2017) reviewed the status of each of these salmonids and concluded that 75% will be extirpated in 100 years or less if present trends continue. Climate change was identified as the over-arching driver of salmonid declines because it exacerbated long-term effects of river alteration and water removal. Drought, however, is likely to be the 'final blow' for many populations because increased length, severity, and frequency of droughts are predicted (Mount et al. 2018).

Policy and management reforms are needed for California's fishes to persist—and even prosper—in extreme drought conditions (Mount et al. 2017, 2018). Moyle et al. (2017) provide specific recommendations for salmonid persistence that include improved protection and management of cold source waters (e.g. spring systems) and the least altered river systems, as well as improved management of altered waterways through a reconciliation ecology approach. The overarching approach assumes that impacts of severe drought can be reduced if the state is adequately prepared and starts managing river systems for drought proactively rather than reactively. The state's iconic salmon and trout will serve as indicators of success of these efforts.

Box 2 Maxims for fish managers about drought. Maxims are statements that should hold true most of the time, without further clarification and are based on the information reviewed in this paper

1. Future droughts will be longer, more frequent, and more severe, creating more stressful conditions for freshwater fishes
2. Climate change and human alteration of aquatic systems combine to increase the negative effects of drought
3. Most fishes can survive natural droughts in their native waters through physiological and behavioural adaptations to changing conditions
4. Different species respond to drought in different ways, so post-drought fish assemblages are hard to predict, especially in highly altered habitats
5. When natural environmental variability is suppressed by human activity, aquatic ecosystems become dominated by a few tolerant fish species and/or by non-native species
6. Fish survive droughts by dispersal or migration to other habitats or by finding refuge in remnant habitats where conditions are physiologically suitable
7. The most abundant fishes in streams in regions with frequent natural droughts are those with the ability to rapidly disperse and recolonize as both adults and juveniles
8. The best drought refuges are large rivers, lakes, spring-fed streams, and deep permanent pools in streams
9. The bigger and more diverse the drought refuge, the more fishes it can shelter
10. Connectivity among habitats is essential for recovery of fish faunas in streams and lakes stricken by drought
11. Ground water is essential for maintaining stream flows and pool refuges through drought
12. Human activity may produce perpetual drought conditions in streams via surface and groundwater abstraction
13. Poor water quality, especially low dissolved oxygen and warm temperatures, followed by predation, are primary causes of fish mortality in refuges
14. Fish assemblages are shaped by historical and contemporary flow regimes, including drought; changes in the severity or frequency of drought alter fish assemblages, with the changes depending on the history and physiognomy of the system
15. Fisheries production might increase via hyperstability as fish become concentrated in the early stages of drought but their catches will decrease in the long run if habitats are unable to support large populations of harvestable fish
16. Translocation of species to new waters and artificial propagation are desperation measures that are unlikely to ameliorate the effects of human-expanded drought

and Bond 2007). Alterations to the frequency and severity of drought coupled with other stressors (e.g. fragmentation, eutrophication, invasions; Mitro 2016) may exacerbate the impacts of drought and affect the fauna that have evolved under historically less dramatic cycles of drought.

Given that responses to flow restoration may be delayed or unpredictable (Ormerod 2009; Wedderburn et al. 2014), long-term data (e.g. Elliott et al. 1997) can reveal potentially important effects of drought (Poff et al. 2003; Matthews et al. 2013). This is particularly true in the context of river regulation to maintain flows (McMahon and Finlayson 2003; Humphries et al. 2008). The effects of a drought can extend beyond the time of when it occurred and induce delayed effects in fish assemblages and populations. Therefore, short-term studies may not account for some of the time-lagged responses observed in fish assemblages in longitudinal studies of gradually drying systems (e.g. Gido et al. 2010). In addition, long-term data are necessary to establish baselines for fish assemblages that naturally shift over time (Magalhaes et al. 2007; Matthews et al. 2013; Magurran and Henderson 2010). Importantly, fish assemblages are dynamic and no one point in time is necessarily indicative of an expected or reference state; this must be considered when sampling streams to establish a presumed baseline. Succession following disturbance is always at some discrete time point in the process and management should respect that all species assemblages are in a constant state of flux as species interact with one another and as the environment changes.

Addressing the fish conservation challenges arising from drought is difficult. We may not be able to predict or even document all the responses of fish and fisheries to drought; managing rivers and lakes is therefore increasingly challenging in a changing world. The quantification of species traits holds potential to identify drought tolerant and intolerant species and sensitive environments to guide drought management responses. For example, Jarić et al. (In Press) used trait and climatic niche data, to compare climate-change susceptible and resilient freshwater fishes in Europe to reveal conservation hotspots; although not specifically focused on drought, they revealed that Mediterranean fishes were most susceptible to climate change, an area that is prone to extreme drought. In addition, Moyle et al. (2013) developed a quantitative protocol for identifying susceptibility of California fishes, both native and non-native, to climate change, which is arguably also a measure of susceptibility to drought that could be expanded to evaluate other jurisdictions.

Knowledge of which species could become at risk under drought scenarios is not necessarily useful if there is no possibility of restoration or remediation. During the wide-spread North American drought of the 1930s, rescuing "stranded" fish (see Nagrodski et al. 2012) was a major activity of fisheries agencies (e.g., LeCompte 1930; James 1934) but there was little effort made to understand if the rescued fish survived or the effects of transplanted fish on the recipient system. Morrongiello et al. (2011) suggested that conservation translocations or ex situ conservation could assist in conserving small populations of species at risk of extinction. Hammer et al. (2013) used ex situ conservation as a last resort but found it difficult, particularly without a plan in place prior to drought. Undisturbed native habitat (White and Rahel 2008) may be more resistant to drought and artificial refuges may be part of restoration plans to allow fish to persist (Hammer et al. 2013). Ahn et al. (2016) evaluated artificial deep pools as manufactured short-term refuges, but the broader application of such methods needs to be explored in different systems with other species and flow regimes. Habitat protection and restoration will be critical to provide systems with the natural features required to be tolerant of drought (Bond et al. 2008). Floodplain restoration, for example, seems to have created enough residual habitat to allow Sacramento splittail (*Pogonichthys macrolepidotus*) to spawn even during drought years (Moyle et al. 2004). Efforts to increase drought resiliency of fish communities (i.e. ensuring a diverse portfolio of genotypes and phenotypes at the level of individual, population, and species; Schindler et al. 2010) will rely on having habitat that is conducive to resilience; in streams, that generally means having adequate flows and natural levels of connectivity across the stream network. Removing obstructions, particularly dams and weirs, and rewilding watercourses will play an important role in drought resilience of many impacted systems (Fencl et al. 2015; O'Connor et al. 2015; Radinger et al. 2018). Otherwise, intolerant species are likely to disappear whereas opportunistic, often non-native, species may proliferate and a new drought-tolerant assemblage may replace the native fauna. This has already manifested throughout the world as flow regimes have given rise to altered fish assemblages (Matthews and Marsh-Matthews 2003; Magalhaes et al. 2007; Gido et al. 2010).

Understanding and anticipating the potential effects of drought in a changing climate (see Guerreiro et al. 2018) should be met with efforts to proactively develop drought management plans that address oncoming changes and, in doing so, avoid reactive management (Crook et al. 2010; Mishra and Singh 2011; Box 1). In some cases, data show that changes to water use strategies must be severe; for example, Falke et al. (2011) suggested a 75% reduction in groundwater extraction was necessary to maintain connectivity essential to the fish community in the drought-stricken Arikaree River system, USA. Given that drought is not just an ecological phenomenon but a socioeconomic one, biological studies represent only a part of an integrated puzzle to establish better management paradigms that are suitable to multiple stakeholders (Nguyen et al. 2016).

Drought-stricken ecosystems can be considered novel ecosystems that challenge management paradigms (Seastedt et al. 2008). Adaptive management is often suggested as an effective framework for managing uncertainty (Folke et al. 2005) but can only be successful with long-term baseline data and an understanding of individual and assemblage responses to habitat change, and yet these data are largely lacking. A paucity of historical data for many locations may lead to shifting baselines regarding scientific and social understanding of the impacts of drought upon fishes (Humphries and Winemiller 2009), potentially resulting in the incremental loss of species diversity over time. Without increased understanding of physiological and behavioural factors that determine the resistance and resilience of species to drought (see Chessman 2013; Whitney et al. 2016a), it will not be possible to set realistic targets for management and restoration of populations and species in the face of increasing drought frequency and severity.

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