



# A general model of temporary aquatic habitat use: Water phenology as a life history filter

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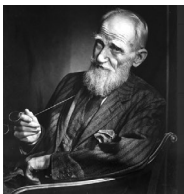
## Abstract

Temporary aquatic habitats are not widely appreciated fish habitat. However, fish navigate the transient waters of intertidal zones, floodplains, intermittent and ephemeral streams, lake margins, seasonally frozen lakes and streams, and anthropogenic aquatic habitats across the globe to access important resources. The selective pressures imposed by water impermanence (i.e., freezing, drying, tidal fluctuations), however, operate similarly across taxa and ecosystems. These similarities are formalized into a conceptual model relating habitat use to surface water phenology. Whereas all necessary life history functions (spawning, foraging, refuge, and dispersal) can be accomplished in temporary habitats, the timing, duration, and predictability of water act as a “life history filter” to which habitats can be used and for what purpose. Habitats wet from minutes to months may all be important—albeit in different ways, for different species. If life history needs co-occur with accessibility, temporary habitats can contribute substantially to individual fitness, overall production and important meta-population processes. This heuristic is intended to promote research, recognition and conservation of these frequently overlooked habitats that can be disproportionately important relative to their size or brevity of existence. There is a pressing need to quantify how use of temporary aquatic habitats translates to individual fitness benefits, population size and temporal stability, and ecosystem-level consequences. Temporary aquatic habitats are being impacted at an alarming rate by anthropogenic activities altering their existence, phenology, and connectivity. It is timely that scientists, managers and policymakers consider the role these habitats play in global fish production.

## KEYWORDS

fish movement and migration, floodplains and wetlands, habitat use, intermittent and ephemeral streams, intertidal zone, phenology and hydroperiod

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## 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 | EPHEMERAL STREAMS TO OCEANS: TEMPORARY AQUATIC HABITATS ARE EVERYWHERE

Temporary aquatic habitats (TAHs) are generally considered to be of marginal value to overall fish production in many aquatic ecosystems, and are easily overlooked by researchers, managers and policymakers (Acuña, Hunter, & Ruhí, 2017). Although relatively few species can breathe air and survive dewatering, all fish on Earth have the ability to move—and this has important implications. Pulses of resources (e.g., food, favourable thermal conditions, spawning substrate) provided by TAHs are in fact widely exploited through adaptive movement behaviour. Reviews and the primary literature provide many examples of TAH use by fishes (Gibson, 2003; Kerezy, Gido, Magalhães, & Skelton, 2017; Leibowitz et al., 2018; USEPA, 2015), yet a conceptual framework linking hydrological characteristics of TAHs and their potential role as fish habitat is lacking. Given the under-recognized role of TAHs and their widespread global distribution, such a framework is a pressing need.

Temporary aquatic habitats are diverse and occur in nearly all ecosystems across the world (Figures 1 and 2). Of all first-order streams below 60° latitude on Earth, 69% are estimated to be temporary, and in arid regions, even large rivers and expansive lakes regularly dry (Peel et al., 2015; Raymond et al., 2013). The Amazon River surges during the rainy season, temporarily flooding vast forests within the lateral floodplain (Goulding et al., 2018), and to some degree, all natural lotic systems have floodplains (Junk, Bayley, & Sparks, 1989). Innumerable ditches and fields are inundated each year, representing an entire class of artificial aquatic habitats (Saulnier-Talbot & Lavoie, 2018). Twice daily Earth's coastline is inundated by the tides, including the ecologically important surf zone (Olds et al., 2018), estuaries, lagoons and tidal flats. In Arctic ecosystems, nearly all shallow waterbodies freeze solid for the majority of the year, yet summer ice thaw transforms the landscape into a vast mosaic of shallow interconnected rivers, lakes and streams (Jones et al., 2013). We intend for the term “temporary aquatic habitat” to include any habitat that is only sometimes aquatic; this broad treatment of the subject is justified to examine similarities in the way fish respond to the phenological properties of aquatic habitats as a consequence of the transitory nature of water.

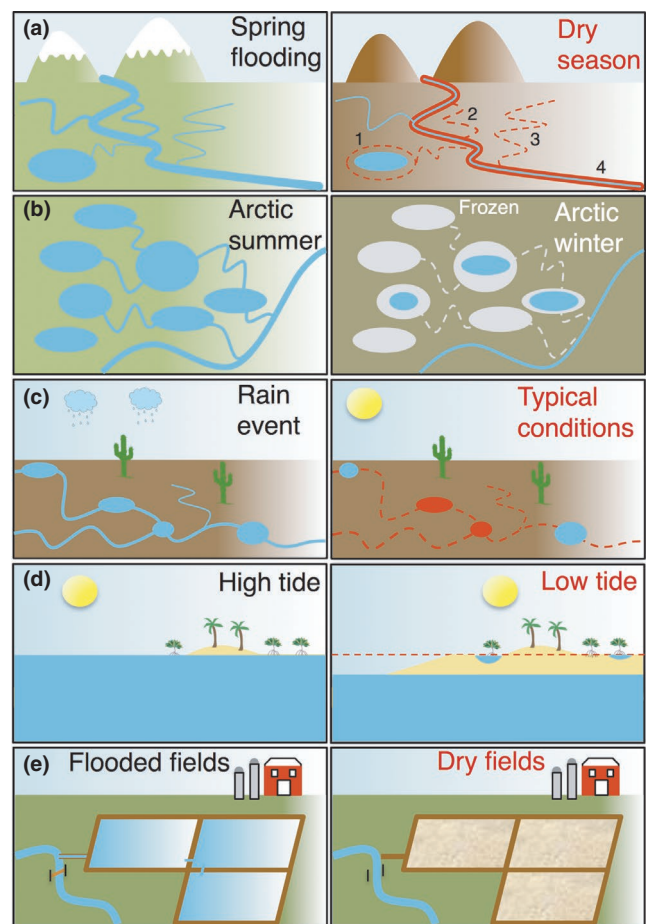
When water is present, how long it is present, and the predictability of water phenology are features that determine the capacity and potential role of TAHs as fish habitat. Because it is the natural variation in hydrology and the complete mosaic of aquatic habitats (not just the permanent ones) to which native taxa are adapted (Leibowitz et al., 2018), alterations to phenological characteristics or access to TAHs could pose significant threats to native fishes. Indeed, the existence and phenology of TAHs are easily disturbed by human water use and development (e.g., dams, bulkheads, forestry, filling wetlands, irrigation), climate change (Jaeger, Olden, & Pelland, 2014), and TAHs are often fragmented from perennial waterbodies (Acuña et al., 2017). Given these already occurring anthropogenic impacts, it is imperative to better understand the contemporary role TAHs serve as fish habitat.

We provide a heuristic framework to explore the life history roles that TAHs serve for fish and how these may scale up in importance

to higher levels of biological organization (e.g., populations, communities and ecosystems). This general model of TAH use is equally applicable in any aquatic ecosystem and is intended to stimulate research, recognition and conservation efforts among fish scientists and managers. Because fish are highly mobile within aquatic environments, our main theme is that habitats need not be permanent to be useful—they just need to be available at the right place and time.

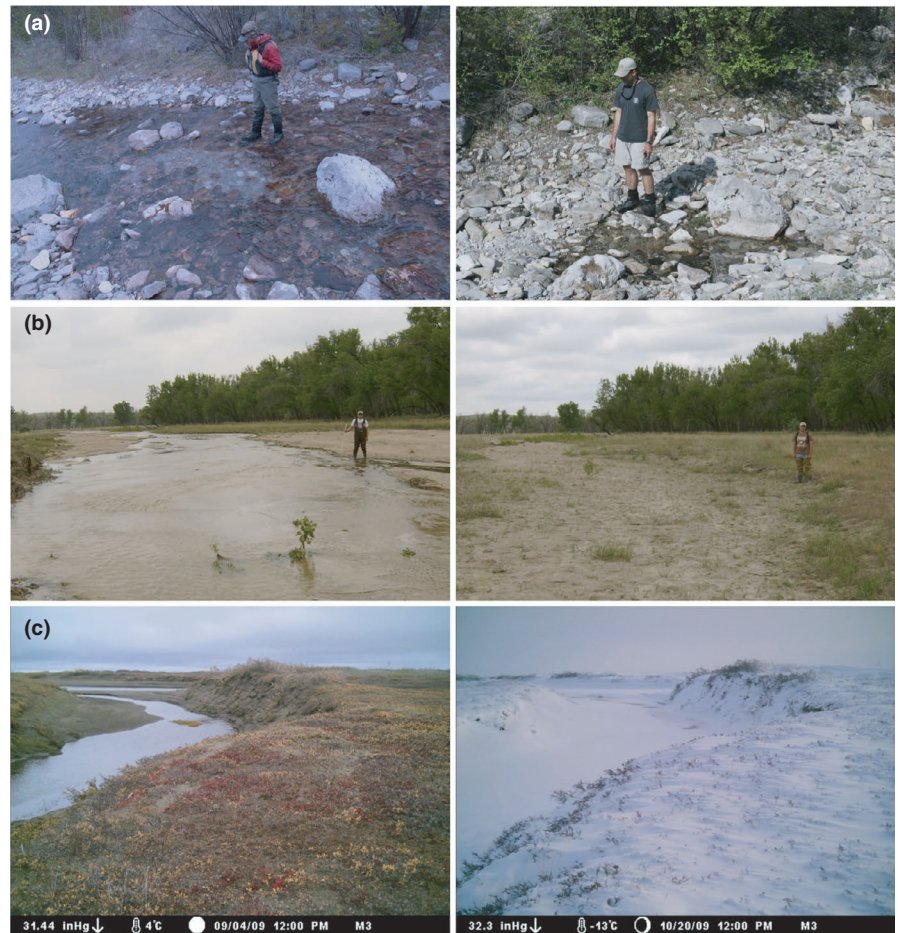
## 2 | HABITAT PERMANENCE ≠ HABITAT IMPORTANCE

Habitat selection is the process by which individuals match changing functional needs with suitable habitats in a heterogeneous



**FIGURE 1** Temporary aquatic habitats occur across the globe in a variety of ecosystems. These include littoral areas that are seasonally inundated (a.1), off-channel or side channel habitats (a.2), intermittent and ephemeral rivers and streams (a.3), and floodplains (a.4). In Arctic and temperate regions, freezing limits availability of liquid water in winter (b, white), while summer conditions provide access to a mosaic of interconnected shallow habitats. In desert and dryland regions, persistent perennial pools represent typical conditions, but are connected episodically by ephemeral channels (c). The tides inundate intertidal habitats (d) twice daily. Anthropogenic features such as flooded agricultural fields and ditches (e), reservoirs and canals are also widely used by fishes

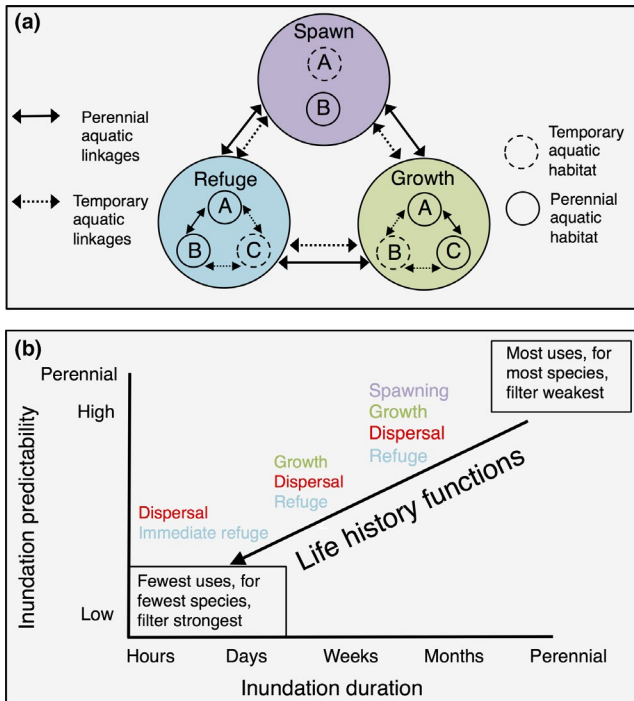
**FIGURE 2** Aquatic habitats are dynamic. Deep Creek, in central Montana, USA (a), is groundwater-fed but only maintains surface flow when soils are saturated (May–September). A salmonid redd is visible. Arikaree River in eastern Colorado, USA (b), is naturally intermittent, but extensive groundwater pumping has led to severe fragmentation that has imperilled native fishes (Falke et al., 2011). Lower reaches are flooded episodically after rain events. In the Arctic Coastal Plains of Alaska, USA (c), habitats become locked in winter ice for up to nine months but are used widely by fishes during the summer. Photo courtesy of M. Lance (a), J. A. Falke (b), and C. D. Arp (c)



and dynamic template of available habitats (McMahon & Matter, 2006; Schlosser, 1991; Schlosser & Angermeier, 1995). Functional needs include spawning, foraging and growth, refuge and dispersal that often require distinct habitat or microhabitats to perform (Figure 3a). Fish movements and migratory behaviours link habitats serving these needs across wide-ranging spatial scales—if functional needs are not being met locally, fish move (McMahon & Matter, 2006). Functional needs also vary across timescales ranging from minutes to years because of intrinsic (e.g., internal cues related to reproduction or ontogeny) and extrinsic (e.g., a flood or a predator) factors. Therefore, specific habitats or microhabitats of small size (e.g., a spawning gravel patch, a rock crevice) can be integral to individual fitness and population productivity even if they are only used for brief periods of time (Baldock, Armstrong, Schindler, & Carter, 2016) or only during specific life stages (Erman & Hawthorne, 1976). Often, a mosaic of habitats is used to meet a single functional need; for example, an individual may track changing prey availability across microhabitats (Figure 3a). This simple way of conceptualizing life history, movement and habitat use is universally applicable to fishes and highlights that (a) functional habitat needs of fishes vary across time, (b) fish move and migrate to meet these needs across time and space, and (c) the spatial arrangement of habitats, their connectivity and characteristics are

the foundation of life history strategies (Schlosser & Angermeier, 1995; Southwood, 1977).

The mosaic of available habitats with different biophysical conditions is the template for behavioural strategies and local adaptations (Southwood, 1977), and includes TAHs just as it does perennial habitats (Figures 2 and 3a). If perennial aquatic habitats used only seasonally or for short periods of time can be vitally important to fishes (this is well recognized in the literature), then why not a habitat that only sometimes exists? Temporary aquatic habitats can serve as spawning, refuge and rearing habitat, or dispersal corridors for a wide range of taxa in marine and freshwater ecosystems (reviewed by Kerezszy et al. (2017) in *Freshwater*, by Gibson (2003) in intertidal habitats). A familiar life history model (i.e., Schlosser, 1991) can be redrawn with TAHs serving any of these functional needs or providing a temporary link between habitat types used for different functions (Figure 3a). Our natural conclusion is that habitat permanence is not necessarily equal to habitat importance. Although water impermanence imposes limitations on the functional roles TAHs can serve, these limitations (and in contrast, the opportunities TAHs can provide) are predictably structured by water phenology in similar ways across taxa and ecosystems (Figure 3b). We explore this relationship and present a general model of TAH use that is equally applicable across the globe—from ephemeral streams to oceans.



**FIGURE 3** Aquatic habitat serves four main functional roles for fish—spawning, growth, refuge and dispersal (a); in many cases, a mosaic of habitats is used for the same functional role (i.e., foraging or refuge in microhabitats A, B, C). Permanent (solid lines) or temporary (dashed lines) aquatic habitats may fulfil all of these needs, and movements used to link habitats across space and time. Yet, the phenology of water within specific habitats imposes limitations to potential functionality, acting as a life history filter (b). All major functions can be accomplished when inundation duration is long and predictable across time, whereas short and unpredictable inundation timing filters potential uses more strongly. Predictably inundated habitats occurring for long periods of time may potentially fulfil multiple life history roles for a single species and for a greater diversity of taxa. Panel a is inspired but modified from Schlosser (1991), Schlosser and Angermeier (1995), and Falke and Fausch (2010)

### 3 | PHENOLOGY OF SURFACE WATER AS A LIFE HISTORY FILTER

Environmental filtering is a heuristic that suggests hierarchically structured biophysical properties of the environment filters species by their traits, leaving only species that pass through all filters to occupy a given area (Poff, 1997). Species sorting is an equivalent concept from metacommunity theory; species are sorted into patches with biophysical properties well suited to their traits (Leibold et al., 2004). In a metacommunity conceptualization at a spatial scale recognizing a discrete TAH as a patch, TAHs are often considered sinks since they do not provide a suite of complementary habitats required for long-term survival (Falke, Bailey, Fausch, & Bestgen, 2012; Pulliam, 1988). However, is the value-laden term “sink” an appropriate characterization of an intermittent stream from which 50% of all trout in a metapopulation are produced (Erman & Hawthorne, 1976), or a floodplain habitat with a 251% carrying capacity (in terms of food) relative to the

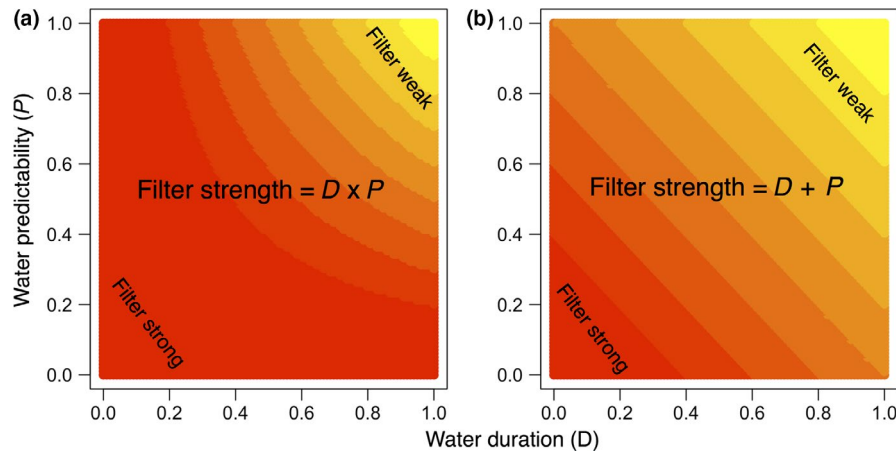
mainstem (Bellmore, Baxter, Martens, & Connolly, 2013), or a seasonally frozen migration corridor required by an entire adult population of fish to access refuge and spawning habitat (Betts & Kane, 2015)?

The above hypothetical example highlights the long-standing issue of scale in ecology in general (Levin, 1992) and meta-theory in particular (Falke & Fausch, 2010). The scale at which ecological problems are considered matters, and examinations across scales or with different conceptual approaches may lead to different insights and conclusions. Patch delineation at spatial scales not including the full range of life history movements for a given fish species would then associate TAHs with concepts and phrases such as “sink,” “high extinction probability,” “second-class” (Acuña et al., 2017) and “ecological trap” (Schlaepfer, Runge, & Sherman, 2002), even while other metrics such as growth and productivity may suggest importance to local fish communities (Labbe & Fausch, 2000).

We propose a conceptual model of TAHs where water phenology acts as a “life history filter” in discrete habitats within the habitat mosaic that an individual is likely to interact with during its lifetime (Figure 3b). This is simply an extension of Poff’s (1997) model of landscape filters, but applied to TAHs and explicitly considering a temporal component to recognize that specific habitats may be only used briefly in time. In Poff’s model, filters are imposed by the environment at different spatial scales, and species may either pass a filter or be constrained by it if it acts strongly relative to the species traits (i.e., warm water is a strong filter for a cold-water specialist). Here, we consider how particular patches of habitat may serve different life history functions as determined by the filtering effects of water phenology—in this sense, it is the full suite of life history functions (not the regional species pool) that is subject to the filter. By “water phenology,” we specifically mean the timing (when), duration (how long) and predictability of these temporal qualities. Habitats with short and unpredictable inundation periods are not useless, but are limited in the number and nature of use(s) to fish (Figure 3b). Habitats inundated for long durations with high predictability may serve many life history functions—the filter is weaker, and such habitats should be widely useful (Figure 3b). We consider water phenology to act as a preliminary filter for fish that can operate at any spatial scale recognized in Poff (1997) because entire watersheds, reaches, channel units or microhabitats may dry or freeze. As TAHs are inundated, they are added to the template of available habitats and can be selected for use. Evolution of life history strategies incorporating TAHs will emerge if their use improves fitness—TAHs are no-less part of the aquatic environment than perennial aquatic habitats.

Although our focus is on life history uses, another prediction stems from this conceptualization. A TAH with a strong life history filter (i.e., short water duration, low predictability) will eliminate many species with “typical” life history needs, but fewer, highly specialized taxa may pass through such filters (Figure 3b). Thus, our proposed model provides predictions at two scales—what species can use a habitat (similar to Poff, 1997) but also, what function(s) the habitat can be used for (Figure 3b). Water phenology has a similar filtering effect at both of these scales.

The potential utility of a given TAH can be conceptualized along two axes of water phenology—predictability and duration—and strength of the life history filter as an additive or multiplicative



**FIGURE 4** Two hypothesized mechanisms of how water duration (D) and water predictability (P) interact and affect the strength of a life history filter (see Figure 3b) in temporary aquatic habitats for fish, a multiplicative interaction (a) or an additive interaction (b). Axes represent an arbitrary scale from zero to 1, from short to long water duration (D; x-axis) and unpredictable to highly predictable water phenology (P; y-axis). The strength of the filter at a given value of D and P depends on the model. The multiplicative model suggests that low values of either water predictability or duration will cause the filter strength to be large, selecting against life history uses that have strict temporal requirements (i.e., spawning, overwintering refuge). This produces a large area of strong filtering (a). By contrast, the additive model suggests that a low value of either metric can be offset by a high metric of the other producing a smaller area of strong filtering (b). We hypothesize that an additive model is more appropriate

function of these two properties (Figures 3b and 4). Water phenology that is unpredictable and of short duration produces the strongest filter against life history uses (bottom left, Figures 3b and 4), whereas the most life history uses, for the most species, are expected in habitats that are highly predictable or inundated for long periods of time (top right, Figure 3b, climaxing at perennial habitat). We hypothesize that filter strength is an additive function of duration and predictability (rather than a multiplicative one) because high predictability can offset short durations (Gibson, 2003) and long durations may offset unpredictability (Peel et al., 2015). Consider predictability and duration of a TAH both as continuous values ranging from 0 (unpredictable and short) to 1 (predictable and long), and a third axis representing filter strength and scaled from 0 (strong filter) to 1 (weak filter, Figure 4). A multiplicative model would suggest a very strong filter (Figure 4) if either predictability or duration was low (i.e.,  $0 \times 1$ , or  $1 \times 0$ ), but empirical observations suggest otherwise. For example, tides inundate intertidal habitats for a few hours (i.e., duration very low), but with impeccable predictability that facilitates adaptive exploitation of the intertidal zone by myriad taxa for growth and refuge. Fewer, highly adapted taxa (represented by ~6 families) also spawn on beaches in synchrony with moon phases and spring tides (Martin & Swiderski, 2001). Temporary aquatic habitats with long durations but low predictability are also widely exploited by opportunistic fish species. Lake Liambezi in Namibia was dry for 22 years; when it flooded in 2009, it was immediately colonized by roughly 50 fish species and now supports a commercial fishery of 2,700 tonnes annually (Peel et al., 2015). Opportunistic behavioural strategies are indeed common in arid landscapes with stochastic flooding events and a scarcity of perennial waterbodies. Although high risks are associated with use of unpredictably inundated TAHs, such risks can yield high rewards (Dodds, Gido, Whiles, Fritz, & Matthews, 2004; Kerezszy et al., 2017).

Variation in water phenology imposes limitations on the potential capacity of a habitat to serve a particular function (Warren, Allen, & Haefner, 1979), while realized use and importance depend on the suite of factors well studied in the field of habitat selection (McMahon & Matter, 2006). Although the life history filter will be strongest in TAHs with short and unpredictable water phenology, this does not imply that those habitats cannot be important. Brief flooding events, lasting for just minutes, may be critical for dispersal across dry habitats and colonization of new habitats (Bramblett & Fausch, 1991; Labbe & Fausch, 2000). We also do not suggest that all predictably inundated TAHs with long durations are necessarily important. As life history needs and phenology vary substantially by taxa, application of this heuristic tool is species-specific, yet it should be informative for all aquatic taxa that depend on liquid water for respiration.

In the following, we highlight how TAHs may serve important life history functions for different fish species to illustrate support for our model (Figure 3b), and highlight cases where TAHs contribute inordinately to fish populations and metapopulations (Table 1). Our intent is to highlight how, why and when TAHs are used, rather than their widely recognized limitations.

## 4 | MECHANISMS OF FUNCTIONAL USE: SPAWNING, GROWTH, REFUGE AND DISPERSAL

### 4.1 | Good childcare: spawning in TAHs

Increasing offspring survival has a profound influence on lifetime reproductive success and population demography in fishes, creating a strong selection pressure to deposit offspring in suitable locations.

**TABLE 1** Examples of studies that quantify the contribution of temporary aquatic habitat to individuals, populations or metapopulations. Studies are listed in order of date published

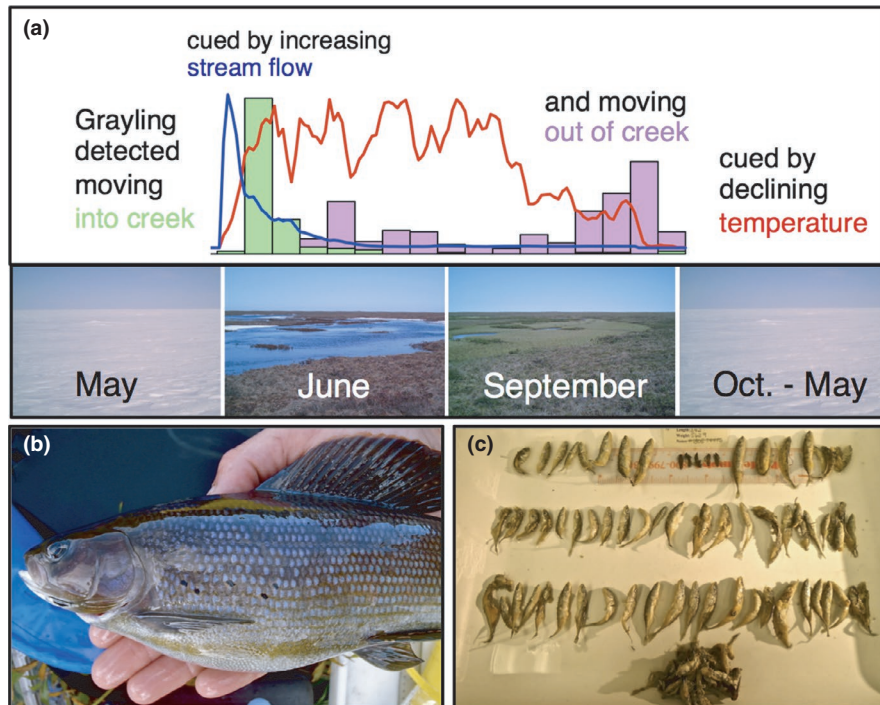
Function	Species	Details	Reference
Spawning	Rainbow trout ( <i>Oncorhynchus mykiss</i> , Salmonidae)	39%–47% of fish within a metapopulation were produced in a single intermittent stream	Erman and Hawthorne (1976)
Growth	Arctic grayling ( <i>Thymallus arcticus</i> , Salmonidae)	Grayling in an irrigation canal had nearly the highest recorded growth rates in Montana	Barndt and Kaya (2000)
Refuge		Overwintering survival ranged from 76% to 100% in four pools	
Growth	Arkansas darter ( <i>Etheostoma cragini</i> , Percidae)	Juveniles grew faster in warmer pools that dried (0.244 mm/day) compared to spring-fed perennial pool (0.21 mm/day). Juveniles hatched 9 days earlier in harsher pools more prone to drying	Labbe and Fausch (2000)
Spawning	Capelin ( <i>Mallotus villosus</i> , Osmeridae)	Beach spawning is preferred strategy; offshore demersal spawning used as a secondary reproductive strategy after conditions on beaches are suboptimal	Nakashima and Wheeler (2002)
Refuge	Orangethroat darter ( <i>Etheostoma spectabile</i> , Percidae)	Avoid mortality from high flows by moving to flooded stream margins; other fish likely die	Dodds et al. (2004)
Growth	Ten species in Australia	Diet breadth substantially increased for fish foraging on floodplains relative to isolated watering holes. Ten species were studied.	Balcombe et al. (2005)
Spawning	Coho salmon ( <i>O. kisutch</i> , Salmonidae)	11%–21% of adults within a metapopulation spawned in intermittent streams	Wigington et al. (2006)
Growth		Smolts rearing in intermittent streams were larger at outmigration than those using perennial streams	
Refuge		Smolt overwinter survival was higher in intermittent streams than perennial streams	
Spawning	Five species in Australia	Recruitment (of five species) documented in stream previously dry for 8 months	Kerezszy, Balcombe, Tischler, and Arthington (2013)
Growth	Arctic grayling	70% of tagged fish used a shallow, seasonally frozen solid lake during the summer; juvenile fish used this habitat for an average of (71 days), nearly the entire ice-free period	Heim et al. (2019)

Temporary aquatic habitats often lack large aquatic predators, provide food for young fish, are warm and contain suitable spawning substrates (Boughton, Fish, Pope, & Holt, 2009). These features often make them ideal spawning habitat when they are predictably available, sometimes promoting higher growth and survival than perennial habitats, and contributing substantially to overall production at the population or metapopulation scale (Table 1).

Temporary aquatic habitats serve as important spawning habitats for many taxa in ecosystems around the globe when they predictably co-occur with species-specific reproductive windows. Floodplain spawning is a characteristic behaviour of many taxa including both native species such as alligator gar (*Atractosteus spatula*, Lepisosteidae) and introduced species such as the common carp (*Cyprinus carpio*, Cyprinidae) (Junk et al., 1989; King, Humphries, & Lake, 2003; Kluender, Adams, & Lewis, 2016). The predictable flooding event provides access to shallow and warm aquatic habitats, abundant food resources and relative safety for offspring development (Junk et al., 1989). Intermittent streams that flow during wet seasons are used in the tropics by representatives of Characiformes, Siluriformes and Cyprinodontiformes

(Alkins-Koo, 2000), and in desert ecosystems such as Australia (where most streams are intermittent or ephemeral) by nearly all native fishes (Kerezszy et al., 2017). In North America, between 11% and 50% of all fish in some salmonid metapopulations are produced in intermittent streams (Erman & Hawthorne, 1976; Wigington, Ebersole, Colvinz, Leibowitzl, & Miller, 2006). Seasonally frozen streams that predictably thaw in the Arctic Coastal Plains of Alaska and the Canadian Arctic are used extensively by Arctic grayling (*Thymallus arcticus*, Salmonidae) and ninespined stickleback (*Pungitius pungitius*, Gasterosteidae) for spawning and provide ideal thermal conditions for rapid offspring growth (Craig & Poulin, 1975; Heim et al., 2016; Figure 5). Many taxa also spawn in anthropogenic aquatic habitats such as ditches or flooded agricultural fields (Barndt & Kaya, 2000; Cucherousset, Carpentier, & Paillisson, 2007). Over one hundred species of fish have been recorded in irrigation ditches in Japan, many of which leave the ditches to spawn in predictably inundated and accessible rice paddies (Natuhara, 2013).

Although a general theme is that inundation periods must be quite long (i.e., long enough for embryonic development) and temporally



**FIGURE 5** Arctic grayling move into and out of a seasonally frozen stream on the Arctic Coastal Plain, Alaska, in close synchrony with changing habitat access related to thawing, flooding and freezing (a). Photographs depict seasonal changes in habitat conditions. Arctic grayling using this stream (b) primarily consumes high-energy content ninespined stickleback (*Pungitius pungitius*) (c) that use the stream network to spawn and forage. Panel c shows the stomach contents of the same individual fish shown in panel b. Eighty-three stickleback were found. Photo courtesy of C. D. Arp (a) and J. J. McFarland (b, c). Data (a) are from Heim et al. (2016), bars in green show initial movements into the stream in 2013 (by week,  $n = 155$  total fish) of fish tagged the previous year. During the week immediately after ice break up, 113 of the 155 of these returning fish entered the stream. Purple bars show final movements out of the stream in 2013 (by week,  $n = 302$  total fish) that includes fish tagged in both 2012 and 2013. During the last week before freeze up, 67 of these fish migrated towards overwintering habitat. Blue and red lines show daily mean discharge and temperature trends. Figure appears in colour in the online version only

predictable for TAHs to serve as spawning habitats (Figures 3 and 4), there are several exceptions. Several highly specialized fish species including the capelin (*Mallotus villosus*, Osmeridae) are adapted to spawn synchronously with high tides and deposit offspring on beaches (Gibson, 2003; Martin & Swiderski, 2001). Although the inundation period is very brief (i.e., hours), the high predictability of the tides (and consistent moist substrates in beach gravel) allows for evolutionary adaptations to exploit this seasonal habitat—consistent with the predictions of our life history filter model (Figure 3b). Alternatively, in the Great Plains region of North America flooding disturbance can be severe, unpredictable and variable in duration and has led to the evolution of highly opportunistic spawning behaviour by native fishes (Dodds et al., 2004). Following floods that can lead to high mortality of recently hatched juveniles, many species are able to immediately reinstate spawning. Some of these prairie species, such as the Arkansas darters (*Etheostoma cragini*, Percidae) provide growth advantages to their young by spawning in intermittent pools that facilitate more rapid growth than perennial pool habitats that are colder (Labbe & Fausch, 2000). Growth advantages are a common advantage provided by TAHs, for both adults and offspring.

#### 4.2 | Warm places to grab a meal: growth advantages

Relative to habitats needed for spawning, refuge and dispersal (needs that generally occur seasonally), foraging habitats are consistently required across time for most taxa. Since growth and size are strongly associated with components of fitness, such as overwintering survival (Quinn & Peterson, 1996) and fecundity, adaptations to maximize growth through habitat selection are common. Indeed, many fish demonstrate complex movement behaviour to exploit “resource-waves”—patchily distributed resources in space and time (Armstrong, Takimoto, Schindler, Hayes, & Kauffman, 2016). Moreover, many species have excessive digestive capacities well adapted to a life of “feast and famine,” allowing for quick assimilation of energy during pulses of food availability (Armstrong & Schindler, 2011). Temporary aquatic habitats provide both short feasts and long-term foraging opportunities, often in synchrony with thermal conditions that maximize physiological growth potential.

Periods of drying have important implications for TAH productivity and nutrient cycling (Bärlocher, Mackay, & Wiggins, 1977; Gerull, Frossard, Gessner, & Mutz, 2011) that may lead to high rates

of food production. Dry periods can pre-condition temporary waters for high productivity during inundation (e.g., a resource pulse), similar to the concept of trophic upsurge in newly flooded reservoirs (Grimard & Jones, 1982). Consequently, prey availability to fishes is often greater in TAHs relative to perennial habitats. Examples include off-channel ponds (Limm & Marchetti, 2009), inundated floodplains (Balcombe, Bunn, McKenzie-Smith, & Davies, 2005; Junk et al., 1989), intermittent streams (Progar & Moldenke, 2002) and tidal flats (Gibson, 2003).

Movements to capitalize on foraging opportunities in TAHs are common in the literature across a wide range of taxa (Kerezszy et al., 2017). Sometimes, small-bodied fish using TAHs for one purpose (e.g., spawning) are closely followed by predatory fish to eat them (McFarland, Wipfli, & Whitman, 2017, Figure 5). This is also true in the intertidal zone, where prey fishes take refuge from open water leading to a distributional shift that is tracked by predatory fishes and avian predators (Calle, Green, Strong, & Gawlik, 2018; Gibson, 2003). Many well-known and recreationally important fish species such as bonefish (*Albula vulpes*, Albulidae) and permit (*Trachinotus falcatus*, Carangidae) regularly access inundated tidal flats with the incoming tide to forage (Murchie et al., 2013). Such movements into TAHs can increase the diversity of forage available to fishes; for example, in Australia diet breadth was much higher and included higher quality prey items when fishes foraged on floodplains, compared to when foraging in isolated waterholes (Balcombe et al., 2005).

Thermal conditions in TAHs are often warmer than nearby perennial habitats, contributing thermal heterogeneity to habitat templates (Figure 6) and providing opportunities for behavioural thermoregulation. This can be especially important for young fish with higher thermal optima relative to adults (Morita, Fukuwaka, Tanimata, & Yamamura, 2010), or during periods of high prey abundance where rapid assimilation of energy is required before the next foraging bout (Armstrong & Schindler, 2011). Shallow lakes in Arctic Alaska that freeze solid in the winter thaw in the spring an average of 17 days earlier than deeper lakes that do not freeze (Arp, Jones, Liljedahl, Hinkel, & Welker, 2015), providing early access to food and warm temperatures for migratory fishes (Heim, Arp, Whitman, & Wipfli, 2019). At daily timescales, juvenile coho salmon (*Oncorhynchus kisutch*, Salmonidae) feed to satiation in the cold thalweg of a river, but move to warm off-channel TAHs to digest food more rapidly (Baldock et al., 2016). Fish using this strategy can substantially increase growth rates (Armstrong et al., 2013). Lastly, relative to perennial pools in the Great Plains, USA, shallow pools with drying potential are often warmest, leading to faster growth relative to perennial pools for the threatened Arkansas darter (Labbe & Fausch, 2000).

#### 4.3 | Staying safe and finding a home: refugia and dispersal

Habitats serving as refugia and dispersal corridors are required at a variety of temporal scales in fishes, both for adults and for offspring. High turbidity and flow in main channels may cue movements into

small tributaries or off-channel habitats where conditions are more favourable (Huntsman & Falke, 2019; Koizumi, Kanazawa, & Tanaka, 2013). These movements may be brief and perhaps hard to observe (Scrivener, Brown, & Andersen, 1994), but may be essential for the survival of young fish that would otherwise be washed downstream and killed (Harvey, 1987). Such short-term refuge in TAHs may be common across arid regions where flash flooding occurs; for example, orangethroat darter (*Etheostoma spectabile*, Percidae) move to flooded stream margins where they are safe from high flows and can quickly re-colonize mid-channel habitats as floods recede (Dodds et al., 2004). Daily refuge movements are also well documented by juvenile fish that move onto tidal flats to avoid higher rates of aquatic predator encounters in deeper water (Gibson, 2003).

Fish also use TAHs as refugia from long-term unfavourable conditions. In the Pacific Northwest where severe winter flooding is common, juvenile salmonids overwintering in intermittent streams can grow and survive at rates higher than those rearing in mainstem habitats (Table 1). In the Arctic, migratory lacustrine–adfluvial Arctic grayling avoid high rates of predation by lake trout (*Salvelinus namaycush*, Salmonidae) by entering a seasonally frozen river during the summer that lacks aquatic predators (Hershey et al., 1997). In this example, grayling also spawn and forage in the river habitat, highlighting that TAHs can serve multiple life history functions simultaneously (e.g., foraging and refuge). In such cases, there should be even stronger selection for behaviours incorporating TAHs into migratory circuits.

Dispersal across TAHs is important for freshwater and marine taxa alike (Figures 2 and 3b). The role of flooding in dispersal is well documented in freshwater fish populations, where individuals in refugia pools can move great distances to colonize new environments during episodic flooding (Labbe & Fausch, 2000). In dryland regions, seasonal and episodic linkages among perennial habitats support important demographic (Falke & Fausch, 2010) and genetic processes vital to functioning metacommunities (e.g., Urban et al., 2008). This is evidenced by the rapid decline of many Great Plains fishes following habitat fragmentation, which prevents dispersal and important rescue effects (Falke et al., 2011; Perkin et al., 2017). In some marine species, spawning migrations are perfectly synchronized with the tidal cycle such that hatching offspring are able to disperse across inundated beaches during spring tides (Gibson, 2003; Martin & Swiderski, 2001).

## 5 | STRANDING: BAD FOR FISH, GOOD FOR ECOSYSTEMS?

The primary risks associated with using TAHs are stranding (or freezing) and potential exposure to high predation rates in shallow-confined spaces (Clavero, López, Franch, Pou-Rovira, & Qeral, 2015; Cucherousset et al., 2007). We do not review stranding extensively (see, Nagrodski, Raby, Hasler, Taylor, & Cooke, 2012), but note that (natural) stranding risk is not fundamentally different than other sources of mortality from an evolutionary perspective. Despite the



impression that stranding is a more calamitous fate, a fish can only die once. Threats to survival are balanced by the evolution of behavioural trade-offs, and if potential benefits outweigh the risks, TAHs will be incorporated into life history movements.

The literature on stranding is, however, dominated by examples of human-caused stranding. Highly irregular and unpredictable dewatering events, like those caused by hydropeaking below dams, appear to be more likely to strand fish than natural and or gradual dewatering (Nagrodski et al., 2012). Fish stranding has also been documented in relation to dewatering flooded agricultural fields (Clavero et al., 2015), and is a common problem in irrigation diversions that entrap fish (King & O'Connor, 2007; Nagrodski et al., 2012; Roberts & Rahel, 2008). In these cases, TAHs can justifiably be considered sink habitats (Pulliam, 1988) or ecological traps whereby environmental cues triggering appropriate behavioural responses are decoupled by rapid environmental change (Schlaepfer et al., 2002). When dewatering or freezing events are predictable or gradual, fish are often able to interpret proximate environmental cues that signal drying or freezing and initiate appropriate behavioural responses (Bradford, 1997; Heim et al., 2016; Figure 5a). Not surprisingly, stranding potential may be greater for non-native species that have not evolved behavioural responses to declining flows that native fish have (King & O'Connor, 2007). At a population level, loss of fish because of stranding appears to be outweighed by the benefits associated with TAH access and growth benefits (Sommer, Harrell, & Nobriga, 2005), but more research on natural stranding events is needed before making general conclusions (Nagrodski et al., 2012).

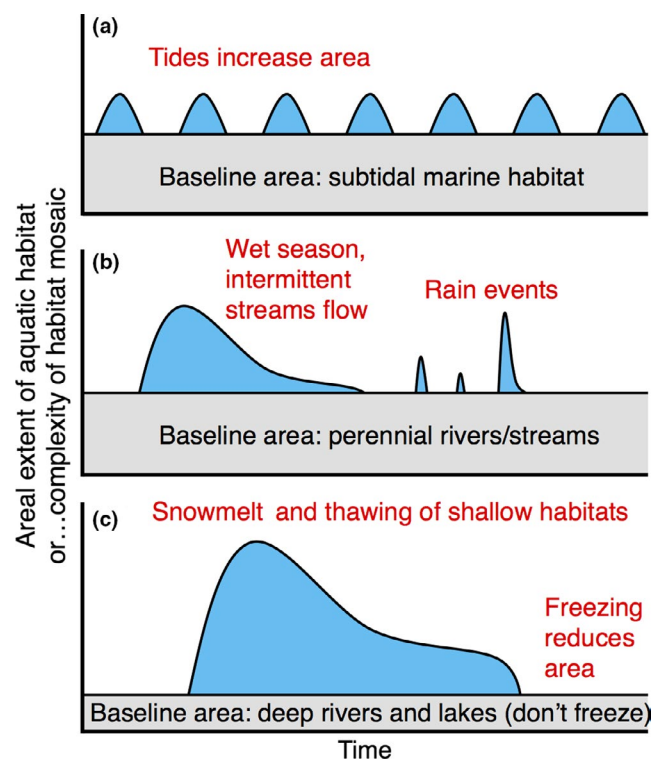
The negative consequences of stranding for fish may provide significant ecosystem services. Stranded fish provide aquatically derived protein subsidies to terrestrial predators, including humans and many bird species (Nagrodski et al., 2012). Just as terrestrially derived resources can subsidize aquatic systems (Wipfli & Baxter, 2010), reciprocal subsidies to terrestrial predators are facilitated by occasional or regular, massive stranding events. Such stranding events are known to occur in the Parana River system of South America, where an estimated 40,000 tonnes of fish are stranded each year (Bonetto, Dioni, & Pignalberi, 1969). Even if not leading to stranding, TAHs that benefit fishes most (e.g., ones with long durations or ones that are predictable) may lead to equally high use by predators that also select habitat according to duration of resource availability (Calle et al., 2018).

## 6 | THE CAPACITY OF AQUATIC ECOSYSTEMS TO SUPPORT FISH

Populations of aquatic organisms, in terms of capacity and performance, are fundamentally tied to the environmental systems in which they evolve (Warren et al., 1979). Temporary aquatic habitats not only increase the areal extent and volume of aquatic habitat, but also increase habitat heterogeneity and connectivity by linking diverse habitat patches (Figure 6). The increased habitat complexity created by TAHs is likely to facilitate diversity in life

history strategies, within and across populations, generating stabilizing portfolio effects (Den Boer, 1968; Schindler et al., 2010). If some fish used TAHs, while others did not, stranding risk would be spread across individuals with different behavioural strategies (Baldock et al., 2016; Heim et al., 2019). At the metapopulation scale, TAHs can contribute substantially to overall production in some years (Table 1), while perennial spawning populations could sustain production in times of poor conditions in TAHs. Complex and complementary habitats may also weaken trophic interactions because resource use among taxa can be partitioned across space, potentially leading to higher aggregate food web stability (Bellmore, Baxter, & Connolly, 2015).

The concept of TAHs as aquatic habitat “supplements” (Figure 6) also provides an interesting link to the concept of trans-ecosystem subsidies—resources (such as food) that are exploited or consumed in ecosystems different from where they are produced (Polis, Anderson, & Holt, 1997; Wipfli & Baxter, 2010). Usually, subsidies are transported by abiotic physical forces (such as the downstream flow of invertebrates from fishless headwater streams [Wipfli, 2005]) and then consumed; yet, we have highlighted here how the consumers themselves may traverse dynamic ecosystem



**FIGURE 6** Temporary aquatic habitats increase the total capacity of aquatic systems by increasing areal extent of habitats, complexity and connectivity within habitat templates used by fish. The marine intertidal zone (a), intermittent and ephemeral streams (b), and seasonally frozen habitats (c) can be considered supplements to the baseline amount of perennial habitats in aquatic ecosystems. Loss of access to these habitats, or alterations to water phenology, will have largely unknown consequences to fish populations

boundaries to acquire resources produced in ecosystems they cannot usually access.

Because we generally have a poor understanding of how TAHs contribute to global fish production, it is difficult to predict the consequences of losses, additions or shifting phenology of these habitats. Across the globe, channelization of major river systems has reduced the availability of floodplain habitats leading to declines in native taxa (Aarts, Brink, & Nienhuis, 2004) and inadequately designed culverts prevent access to small stream habitats (Warren & Pardew, 1998). In Arctic regions, ice-road construction associated with oil and gas development sites has potential to disturb hydrological connectivity to important seasonally accessible lakes and streams during the summer (Arp et al., 2019). In marine environments, sea-walls are being built at unprecedented rates that may eliminate or prevent access to the intertidal zone (Morris et al., 2018).

A shifting climate and a growing demand for water are also anticipated to increase the prevalence of intermittent streams and the duration of dry periods, changing natural water phenology that organisms are adapted to (Jaeger et al., 2014; Larned, Datry, Arscott, & Tockner, 2010). Dryland region watersheds of N. America are expected to become more fragmented across space and time (Perkin et al., 2017), with increases of up to 27% in the frequency of no-flow days by mid-century (Jaeger et al., 2014). Changing phenology of TAH availability may have important consequences, especially if it decouples temporal availability from the phenology of life history needs by locally adapted taxa. Such changes could render formerly important TAHs as ecological traps (Schlaepfer et al., 2002). Changes to other types of TAHs, such as seasonally frozen Arctic streams and lakes, may shift substantially in the timing and duration of freezing, becoming more similar to perennial waterbodies (Arp et al., 2015). Given these widespread ecosystem alterations, gaining a better understanding of TAHs—from a fisheries perspective—is an important research priority.

## 7 | THE BIG PICTURE: RESEARCH NEEDS AND RESOURCE MANAGEMENT

### 7.1 | Research needs

Our aim is that this conceptual framework, linking life history to water phenology, will stimulate further research and an increased awareness of the potential role TAHs can play in fish production and conservation. First, we emphasize the importance of publishing documented use of TAHs in the peer-reviewed literature. Raising broader awareness of the role that TAHs play in aquatic ecosystems is imperative to fostering increased recognition, research and conservation efforts (Hunter et al., 2017; Larned et al., 2010). Regional journals are excellent venues to make observations accessible to other scientists and managers to support more broad consideration of TAHs in fisheries management plans. However, simply capturing fish in TAHs should not be interpreted as evidence of functional importance. Just as habitat permanence is not equal to habitat importance, it is also true that habitat use is not always reflective of habitat importance (Van Horne, 1983).

Our second recommendation is to increase efforts to quantify individual, population and ecosystem-level benefits of fish using TAHs. Although TAHs no doubt supplement available perennial habitat in different ways across ecosystems (Figure 6), there are few studies that have quantified the relative contribution to fish production. But those that have done so often reveal TAHs inordinately contribute to overall production (Table 1). It is important to note, however, that quantifying “relative” contribution implies that the benefits (growth, production, etc.) can be partitioned between TAHs and perennial habitats. In some cases, this is feasible because some populations within metapopulations use TAHs, while other populations use only perennial waters (Wigington et al., 2006). This sets up a nice contrast for comparative analyses. In other cases, entire populations or metapopulations occur within macrohabitats that are classified as TAHs (i.e., obligate use of TAHs) and this distinction becomes less clear. Nearly all lotic habitats in Australia are intermittent to some degree (Kerezszy et al., 2017); here, 100% of production is justifiably attributable to TAHs, just as it is in interrupted streams of N. America (Dodds et al., 2004), or perhaps obligate floodplain spawning species (King et al., 2003). Yet, relative contribution may still be an applicable concept, if distinct habitat patches that dry or freeze (Figure 1) are evaluated for their functional roles and contributions relative to perennial waters within mosaics of habitat patches (Davis, Kerezszy, & Nicol, 2017; Labbe & Fausch, 2000).

When TAHs support spawning populations, offspring can be directly assigned to TAH origins and compared with those originating from perennial sources. Direct sampling of emigrating fish (Craig & Poulin, 1975), tagging (Ebersole et al., 2006) or remote monitoring systems such as passive integrated transponder antenna are useful methods for this purpose. Another promising approach is the use of genetic tools to assign fish to populations of origin (Manel, Gaggiotti, & Waples, 2005). Genetic and genomic tools may have far-reaching applicability in the context of TAHs, to estimate effective population size and effective number of breeders (Benestan et al., 2016), identify the contribution of TAH breeding populations to overall genetic diversity, and identify genes under selection across TAHs with varying phenological properties. Temporary aquatic habitats, where water phenology is expected to create strong selection pressures and local adaptations (Figure 3b), may also be excellent natural study systems to evaluate emerging concepts in eco-evolutionary dynamics (Pelletier, Garant, & Hendry, 2009).

In TAHs used for growth or refuge, indirect measures of individual fitness (e.g., growth, survival, body condition) will be useful to quantify the contribution of TAHs (Moyle, Marchetti, Baldrige, & Taylor, 1998; Wigington et al., 2006). Newer technologies in fish physiology, such as bioelectrical impedance analysis to non-lethally estimate lipid reserves of individuals (Cox & Hartman, 2005), may be particularly useful, especially if paired with individual movement and habitat use data.

The concepts presented here (e.g., Figures 3, 4 and 6) present new avenues for modelling approaches, synthetic analyses and data-driven studies to understand the role of TAHs in fish populations. How much physical area and habitat complexity do TAHs contribute

at local, regional and global scales (Figure 6)? How do TAHs contribute to thermal heterogeneity in the aquatic system and how might behavioural thermoregulation influence carrying capacity of a system? How much do TAHs contribute to overall fish production, and what are the consequences of their loss? How do components of water phenology influence life history filtering, species diversity, community composition and higher levels of biological organization in nature (Figures 3b and 4)? Controlled experiments and mesocosm studies would also be especially fruitful approaches for further research. Assessing results from a common conceptual perspective (perhaps, Figure 3b) will help move from a collection of case-studies to more foundational conclusions about the role of TAHs in fish production.

In all cases, relating production or individual growth estimates back to water phenology will be essential to provide empirical support for theory, better understand conditions substantiating TAH contributions, and make predictions in new environments. Replication across space and time will also be necessary, since temporal variation in production is to be expected—in some years, TAHs could serve as population “sinks” but perhaps in others contribute inordinately to metapopulations. To this end, we recommend the use of inexpensive temperature and water-level loggers to characterize water phenology and temperature regime. In small streams, it is easy to measure discharge using the velocity–area method (Buchanan & Somers, 1969), and rating curves can easily be developed to predict continuous flow estimates from loggers. If discharge cannot be measured, sensors that can detect intermittency are recommended to characterize the phenology of water presence in TAHs (Chapin, Todd, & Zeigler, 2014). Lastly, the use of time-lapse cameras has also been useful in our experience to depict the seasonality of water presence and produce striking visual contrasts for presentations (Figure 2).

## 7.2 | Fisheries management in TAHs

Many scientists and managers have called for a unique approach to management of TAHs (Acuña et al., 2017; Larned et al., 2010), recognizing that their ecology is inherently different than perennial waters, yet integral to overall aquatic ecosystem function. The recommendations in Acuña et al. (2017) provide an excellent framework for broad-scale management of TAHs, and we urge fisheries managers to incorporate these suggestions into management plans where feasible. In summary, these suggestions include (a) mapping the distribution of TAHs across the landscape, (b) raising broader awareness of TAHs, (c) protection and preservation of natural hydrological variation and (d) restoration of degraded reaches. Of particular importance is raising awareness of the importance of TAHs to fish populations of interest, and effectively quantifying their overall impact and economic value will help to elevate the political priority of their conservation (Lynch et al., 2017). A key component of this approach is to recognize that flow intermittency is not necessarily a stressor, but is an innate and important component of natural aquatic systems, which may have important implications for fish populations (Fausch,

Torgersen, Baxter, & Li, 2002). Managers should not attempt to convert TAHs to permanent ones, but to preserve the natural variation in flow and ecosystem function of these natural features. While flow restoration continues to be a powerful tool in freshwater fish conservation, flow augmentation should be done with care (Acuña et al., 2017). Augmentation of flows beyond natural levels disturbs natural processes of drying and freezing, and changes phenology that may lead to the proliferation of non-native species that have distinct ecological advantages in stable conditions. Additionally, maintaining access to TAHs that serve functional roles will be increasingly important as roads fragment dendritic riverscapes and seawalls limit intertidal zone access (Morris et al., 2018).

The fact that rare or unique features in riverscapes can be disproportionately important to stream fish emphasizes the need for judicious use of continuous sampling in space and time. (Fausch et al., 2002)

In addition to broad-scale protections of TAHs (Acuña et al., 2017; Hunter et al., 2017), more focused efforts to identify specific TAHs that are disproportionately important to fish populations of interest are justified. Environmental regulations and federal protections of TAHs are varied (Leigh et al., 2015) and often controversial (Acuña, 2014). For example, a revision of the Clean Water Act in the USA in 2015 to explicitly include some forms of temporary waterbodies (Clean Water Rule: Definition of “Waters of the United States”, 2015) has been met with substantial political resistance. Although this regulation was based on thorough scientific review by the US Environmental Protection Agency (USEPA, 2015), and was praised by fisheries conservationists (Bigford, 2015), recent legislation seeks to deregulate protection for many wetlands and all ephemeral streams in the USA (Revised definition of the “Waters of the United States”, 2018). While broad-scale policy changes to protect riverscape scale processes are ideal (Acuña, 2014), implementing them can be challenging and there remains a strong need for directed management of critical habitats at the local scale. The concept of a life history filter will be useful to specifically identify TAHs with potentially outsized importance to local fish populations that can be targeted for local conservation efforts.

We suggest a hierarchical approach to identify and conserve TAHs that are particularly valuable to fish populations of interest that broadly includes identification, understanding function and protecting that functionality. What habitats are important, why are they important and when are they important? Close examination of satellite imagery and hydrography layers in a geographic information system are useful tools to identify potentially important TAHs. Channel morphology and substrate can often be evaluated coarsely, and locations of potential importance can be demarcated. Furthermore, local knowledge of regional fisheries biologists will be integral to evaluate species- and population-specific habitat requirements, and the spatial distribution of habitats that might meet these requirements. For example, if it is known that a population is recruitment-limited because of inadequate spawning habitat, this

might provide context in which intermittent or ephemeral streams could be particularly important (Boughton et al., 2009; Erman & Hawthorne, 1976). By evaluating local patterns in water phenology, targeted on-site sampling might be conducted to document use, and further studies carried out to understand importance. In the case of TAHs, “timing is everything” and we believe many potentially important fish habitats remain unknown to fisheries managers simply because when they are wet do not coincide with fieldwork season. For example, a wealth of literature is available for bluehead (*Castostomus discobolus*, Catostomidae) and flannelmouth suckers (*C. latipinnis*)—yet a recent study documented an unprecedented degree of spawning activity in an intermittent stream that provides a new perspective for conservation efforts in the Colorado River basin (Hooley-Underwood, Stevens, Salinas, & Thompson, 2019). Indeed, focused studies targeting TAHs often reveal surprisingly high use and importance.

## 8 | CONCLUSIONS

It is the complexity, stochasticity and integrity of habitat templates that have facilitated the ecology and evolution of fish populations globally (Southwood, 1977)—habitat permanence is not inherently good or bad (Acuña et al., 2017). Although fisheries management has primarily focused on perennial waterbodies, there is justification to specifically include TAHs in fisheries management plans, monitoring and environmental impact assessments. This will require broader recognition of TAHs as fish habitat and focused research efforts to quantify their contribution to global fish production. Fish and associated fisheries will benefit if the notion that TAHs are “second-class” habitat is abandoned (Acuña et al., 2017), in favour of a balanced perspective recognizing that the evolutionary history—and future—of global fish populations is a function of the complete aquatic environment, not just the permanent part. By considering water phenology as a life history filter, we may begin to recognize the opportunities and benefits provided by this diverse group of aquatic habitats, instead of their limitations.

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