



Fish out of water: Aquatic parasites in a drying world

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ARTICLE INFO

Keywords:

Intermittent rivers
Refuge pools
Freshwater fish
Habitat fragmentation
Disease transmission

ABSTRACT

Although freshwater ecosystems are among the most diverse and endangered in the world, little attention has been paid to either the importance of parasitic disease as a threatening process for freshwater organisms, or the co-extinction risk of freshwater parasites. In this review, we use theoretical and empirical studies of host/parasite interactions to examine these issues, particularly with respect to the threat posed by climate change to fish and parasite communities in intermittent rivers. Intermittent rivers are those that cease to flow at any point in time or space, with isolated pools providing ecological refuges for freshwater biota between streamflow events. Intermittent rivers are the dominant river type in arid, semi-arid and Mediterranean regions; areas of the world that have experienced dramatic decreases in streamflow as a result of climate change. Reduced streamflow decreases the number, size and connectivity of refuge pools in intermittent rivers, with important consequences for free-living aquatic organisms, particularly fishes, and their parasitic fauna. As a result of more frequent and sustained periods of no flow, parasite diversity within refuge pools is expected to decrease, with a concomitant increase in the prevalence and intensity of those parasite species which do survive, particularly host generalists. Decreased connectivity between refuge pool communities should increase the spatial modularity of host/parasite interactions, leading to a greater structuring of host and parasite communities along the river. This increases the probability of species loss (for both hosts and their parasites), as local extinctions cannot be reversed by colonisation from other localities.

1. Introduction

Freshwater environments are extremely biodiverse. Although freshwater rivers, lakes and wetlands constitute only 0.8% of the surface area and approximately 0.02% of the habitable volume of the Earth, they contain almost 10% of known free-living animal species, and approximately 30% of vertebrate species (Dawson, 2012; Wiens, 2015). Marine environments constitute 70% of the Earth's surface area and over 99% of habitable volume, yet the species richness of freshwater actinopterygian fishes (estimated at 15,150 species) is slightly greater than that of marine fishes (14,740 species) (Dawson, 2012). The parasite fauna of marine and freshwater environments have been less comprehensively studied, but Poulin (2016) compared the ratios of number of parasite species to number of genera in marine and freshwater fishes from 14 host-parasite checklists, and found evidence for a greater diversification of freshwater parasites than of marine parasites.

Freshwater is essential to human life, so human settlements have traditionally been along rivers and wetlands. This unfortunate confluence of exceptionally high biodiversity and proximity to people is a major reason that declines in freshwater species have been consistently

greater than those in terrestrial or marine biomes (Reid et al., 2019; Dudgeon, 2019). According to the latest data from the IUCN Red List, 24.6% of assessed freshwater species are currently classified as threatened. Among fishes, the proportion of threatened species is even higher; 27.0%, compared with 7.6% of assessed marine species (IUCN, 2019). The principal threatening processes responsible for this loss of freshwater biodiversity are invasive species, river regulation, habitat loss, pollution, over-exploitation and global climate change (Dudgeon et al., 2006; Arthington et al., 2016).

The isolated and fragmented nature of freshwater environments means that they are particularly vulnerable to the effects of climate change. In addition, freshwater organisms have a limited ability to shift their range in response to climate change, especially when river orientation does not match climate trends (James et al., 2017), and a number of studies have documented the potential adverse impacts of a changing climate on freshwater organisms, particularly freshwater fishes (e.g. Daufresne and Boët, 2007; Ficke et al., 2007; Comte et al., 2013; Beatty et al., 2014). Most of these studies have examined the effect of increasing water temperature on cold water fish communities in perennial, northern hemisphere rivers. However, intermittent (non-

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<https://doi.org/10.1016/j.ijppaw.2020.05.003>

Received 17 March 2020; Received in revised form 4 May 2020; Accepted 4 May 2020

Available online 25 May 2020

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perennial) rivers likely account for at least half of the global river network (Datry et al., 2014, 2016a) and in these rivers, distributed particularly throughout arid, semi-arid and Mediterranean climatic regions, reduced streamflow, rather than increased temperature, will be the major threat to freshwater fishes (Beatty et al., 2017). Compared with marine and terrestrial environments, the impacts of climate change on parasitic diseases of freshwater animals have received relatively little attention and, of those studies that have been carried out, most have concentrated on the effects of increasing temperature rather than altered hydrology (e.g. Dobson and Carper, 1992; Marcogliese, 2008; Marcos-López et al., 2010; Löhmus and Björklund, 2015; although see Marcogliese, 2001, 2016).

In this review, we examine the effects of decreased streamflow on the parasites of freshwater fishes in intermittent rivers. Because so little is known about the parasite fauna of fishes in intermittent river systems, we use theoretical and empirical studies of host/parasite interactions in other fragmented habitats to guide predictions. We start with a brief description of the ecology of intermittent river systems; discuss how this may affect parasites and the dynamics of parasitic disease; investigate the impacts of climate change on river ecology and parasite transmission in intermittent systems; and finally consider conservation and management implications, both for freshwater fishes and for their parasite fauna.

2. The ecology of intermittent rivers

Intermittent rivers (also called temporary, non-perennial, ephemeral, seasonal or episodic rivers; see glossary in Table 1) are those that cease to flow or become dry at any point in time and space. Tooth (2000) estimated that intermittent rivers constitute more than 30% of the total length and discharge of the global river network, but this estimate did not consider low order (headwater) streams; when these are included, intermittent rivers may make up more than 50% of all rivers throughout the world (Datry et al., 2014). Intermittent rivers are the dominant river type in arid, semi-arid and Mediterranean regions (Jaeger et al., 2014; Skoulikidis et al., 2017), but also occur in most terrestrial biomes between 84°N and S latitude (Larned et al., 2010). For example, up to 40% of total river length in France, more than half of river length in the United States, Greece and South Africa, and approximately 70% of river length in Australia is intermittent (Datry et al., 2014).

Commonly used conceptual models in river ecology emphasise the importance of hydrological continuity along the length of the river (river continuum concept; Vannote et al., 1980) and its disruption by river regulation (serial discontinuity concept; Ward and Stanford, 1983); or of lateral (flood pulse concept, Junk et al., 1989) or vertical (hyporheic corridor concept; Stanford and Ward, 1993) continuity in

structuring aquatic communities. None of these models, however, adequately capture the nature of intermittent rivers, which are characterised by shifting mosaics of lotic (flowing), lentic (standing) and terrestrial habitats (Larned et al., 2010; Datry et al., 2014). The spatial arrangement, turnover and connectivity of these habitats are governed by repeated sequences of river flow, flow cessation and drying (Fig. 1). The aquatic biota of an intermittent river can therefore be considered as a dynamic metacommunity, with isolated pools or waterholes, often with substantial groundwater inputs, providing ecological refuges when flow ceases and the river dries; and connections among these isolated patches restored when streamflow resumes (Magoulick and Kobza, 2003; Sheldon et al., 2010).

Metacommunities are structured by an interplay between environmental filtering, where the species composition of a site is determined by abiotic factors and biotic interactions; and dispersal, where species composition is determined by the movement of individuals among sites. In intermittent rivers, the relative importance of these processes varies temporally, with environmental filtering structuring refuge pool communities during the lentic phase, and dispersal from refuge pools during the lotic phase restoring community composition along the river (Datry et al., 2016b). Aquatic communities in disconnected refuge pools usually begin as depauperate subsets of the lotic community (Larned et al., 2010), with progressive loss of species as the lentic phase continues (Datry, 2012). Although a wide range of factors have been suggested to influence the species composition of fish communities in refuge pools, including prior dispersal, habitat structure, water quality, predation and competition (Magoulick, 2000; Davey and Kelly, 2007; Strauch et al., 2015), the potential importance of parasites and parasitic disease has rarely been considered.

2.1. Parasites and parasitic disease in intermittent rivers

The spatial and temporal variability of intermittent rivers is likely to have a major influence on parasite diversity and abundance, and on the dynamics of parasitic disease, because of direct effects on parasite free-living stages and indirect effects on freshwater fishes and other aquatic hosts. The life history strategy of parasites will therefore be a key determinant of the extent of these effects. For parasites of fishes, this means not just host specificity (specialists or generalists), whether life cycles are direct or indirect and how transmission occurs, but also whether parasites are autogenic (fishes are the definitive host) or allogenic (other vertebrates (usually terrestrial) are the definitive host) (Esch et al., 1988).

Intermittent rivers typically have a lower taxonomic diversity, although higher rates of endemism, of freshwater fishes and aquatic invertebrates than perennial rivers (Tedesco et al., 2013; Datry et al., 2014). As far as we are aware, there have been no comparative studies

Table 1

Glossary of terms used throughout the text.

Term	Definition
Dispersal	With respect to metacommunity dynamics, the movement of individuals from one local community to another
Diversity	Typically measured by the species richness or evenness of a region. When the region can be subdivided into different localities, alpha (α -) diversity is the diversity within a locality, beta (β -) diversity is the diversity between localities) and gamma (γ -) diversity is the total regional diversity
Environmental filtering	The loss of species from a local community due to abiotic factors or interactions with other species
Habitat fragmentation	Transformation of one continuous habitat into smaller patches, isolated from each other by a matrix of habitats unlike the original
Intermittent river	River that ceases to flow or become dry at any point in time or space. Sometimes used in a more restricted sense to mean river that has regular, seasonal periods of flow and no flow.
Lentic	Referring to standing water (e.g. lakes, ponds and swamps)
Lotic	Referring to running water (e.g. rivers and streams)
Metacommunity	A set of local communities that are linked by dispersal
Modularity	The extent to which a network is divided into groups of nodes that interact more strongly with each other than with nodes outside the group
Nestedness	With respect to community structure, nestedness occurs when communities with smaller numbers of species are subsets of communities with larger numbers of species
Perennial river	River that flows continuously throughout its length in years with normal rainfall
Refuge habitat	Habitat that conveys spatial and temporal resistance or resilience to communities affected by disturbances
River reach	Section of river or stream along which similar hydrological conditions exist

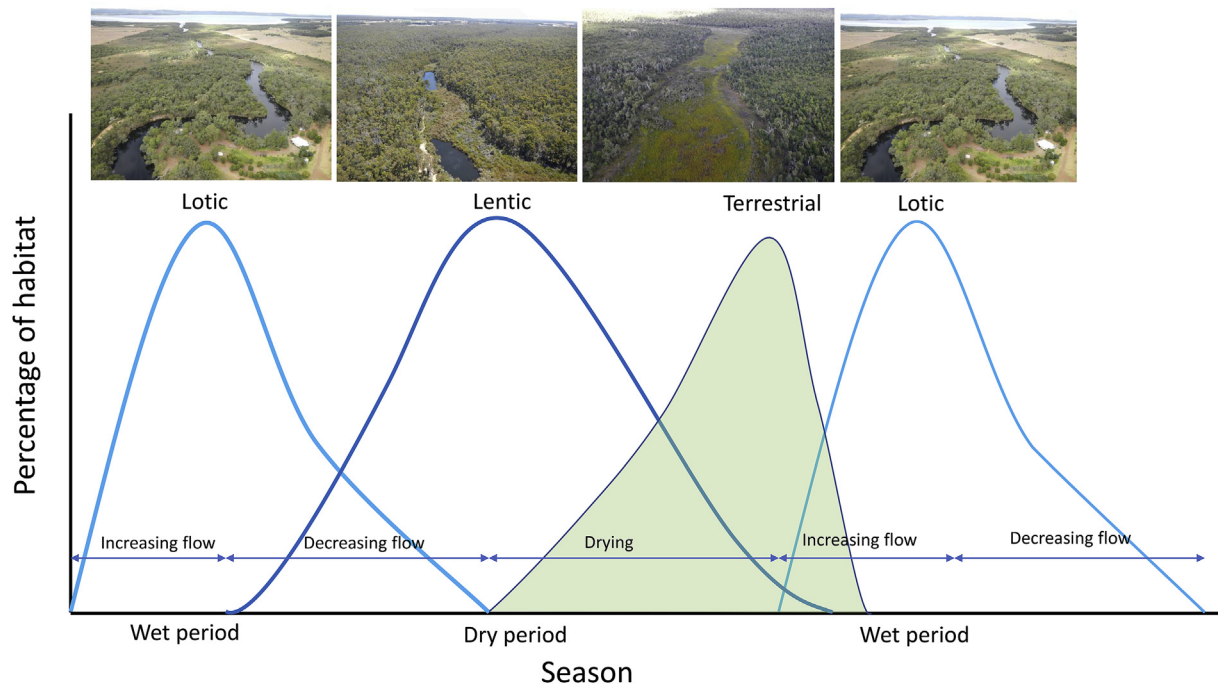


Fig. 1. Conceptual diagram showing alternating cycles of flow, flow cessation and drying in intermittent rivers, with associated changes in the percentage of lotic, lentic and terrestrial habitats (adapted from Datry et al., 2016).

of the diversity of parasites in intermittent and perennial rivers in the same geographic region, or in intermittent and perennial reaches of the same river. However, using the fish host/parasite datasets compiled by Poulin (2016), with geographic region as a proxy for the likelihood of intermittent or perennial river systems, intermittent regions have fewer parasite genera (5.5, 95% CI 4.9–6.0) and species per host (6.2, 95% CI 5.5–6.8) than perennial regions (10.7, 95% CI 9.4–12.0; 12.7, 95% CI 11.1–14.3, respectively). Comparisons within a more restricted (although still substantial) geographic range corroborate this pattern. Lymbery et al. (2010), for example, found 44 putative species of parasites in 18 different species of fish in the largely intermittent river systems of south-western Australia, while Dove (2000) by contrast, recorded 109 different parasite species in the same number of fish species from more perennial systems in Queensland, on the east coast of Australia.

Isolated refuge pools in the lentic phase of an intermittent river constitute a fragmented landscape for the parasite metacommunity. Theoretically, this should decrease parasite species diversity within pools (α -diversity), due to environmental filtering of host species, and increase diversity among pools (β -diversity), because of stochastic variation in host communities. The extent to which overall parasite species diversity in the river (γ -diversity) is affected by flow intermittency will depend on the temporal dynamics of the system; the longer the inter-flow period, the greater the chance that some refuge pools will be lost and the more the long-term stability of the parasite metacommunity will depend on dispersal and re-colonisation once flow resumes and the lotic phase is re-established (Sheldon et al., 2010). The loss of aquatic host species in refuge pools would be expected to favour generalist over specialist parasites, and possibly allogenic over auto-genic species, as increased terrestrial habitat during the lentic phase may increase predation on aquatic hosts by terrestrial predators (Datry et al., 2016b). This may lead to a different community structure in intermittent rivers than in perennial rivers, but there are no empirical studies which have tested these predictions.

In contrast to species richness, parasite abundance within refuge pools is expected to increase for a number of reasons. First, reduced water flow has consistently been associated with increased prevalence

and intensity in parasites that use free-swimming stages for transmission, such as the copepods *Lernaea cyprinacea*, *Ergasilus celestis* and *Salmincola edwardsii*; the trematode *Crepidostomum farionis*; the monogenean *Pseudodactylogyrus anguillae*; the nematode *Rabdochona* sp.; and the myxozoan *Myxobolus cerebralis* (Voth et al., 1974; Medeiros and Maltchik, 1999; Barker and Cone, 2000; Hallett and Bartholomew, 2008; Mitro, 2016). Second, an increase in host density in refuge pools should increase prevalence and intensity in directly-transmitted parasites, as has often been reported, particularly for cultured fishes (Pickering and Pottinger, 1989; Krkošek, 2010; Jansen et al., 2012). Pure density-dependent transmission, however, may be less common in natural populations (Renwick and Lambin, 2013), which would reduce this effect. Bagge et al. (2004), for example, found no influence of host density on the abundance of four monogenean species on crucian carp (*Carassius carassius*) and suggested that density was not relevant above a certain threshold, while Johnson et al. (2011) found frequency (rather than density)-dependent transmission of the monogenean *Gyrodactylus turnbulli* in guppies (*Poecilia reticulata*), which they attributed to the social behaviour (i.e. shoaling) of the fish. Finally, the intensity of predatory interactions among free-living species (both aquatic and terrestrial) increases in refuge pools (Magoulik and Kobza, 2003; Datry et al., 2016b), which may increase the abundance of parasites which utilise trophic transmission, but only if all definitive and intermediate hosts are present in the pool or (for allogenic parasites) utilise the pool for predation.

3. Effects of climate change on parasites and parasitic disease in intermittent rivers

In intermittent rivers, sequences of river flow, flow cessation and drying are intrinsic features of the natural flow regime. Fishes and other free-living aquatic species in these systems have evolved a range of morphological, physiological, behavioural and life history adaptations to this predictable hydrological variation (Aspin et al., 2018), and the same is likely true of parasitic species. Climate change, however, may lead to extreme and unpredictable variation in the natural hydrology of intermittent rivers, with potentially severe consequences for the species

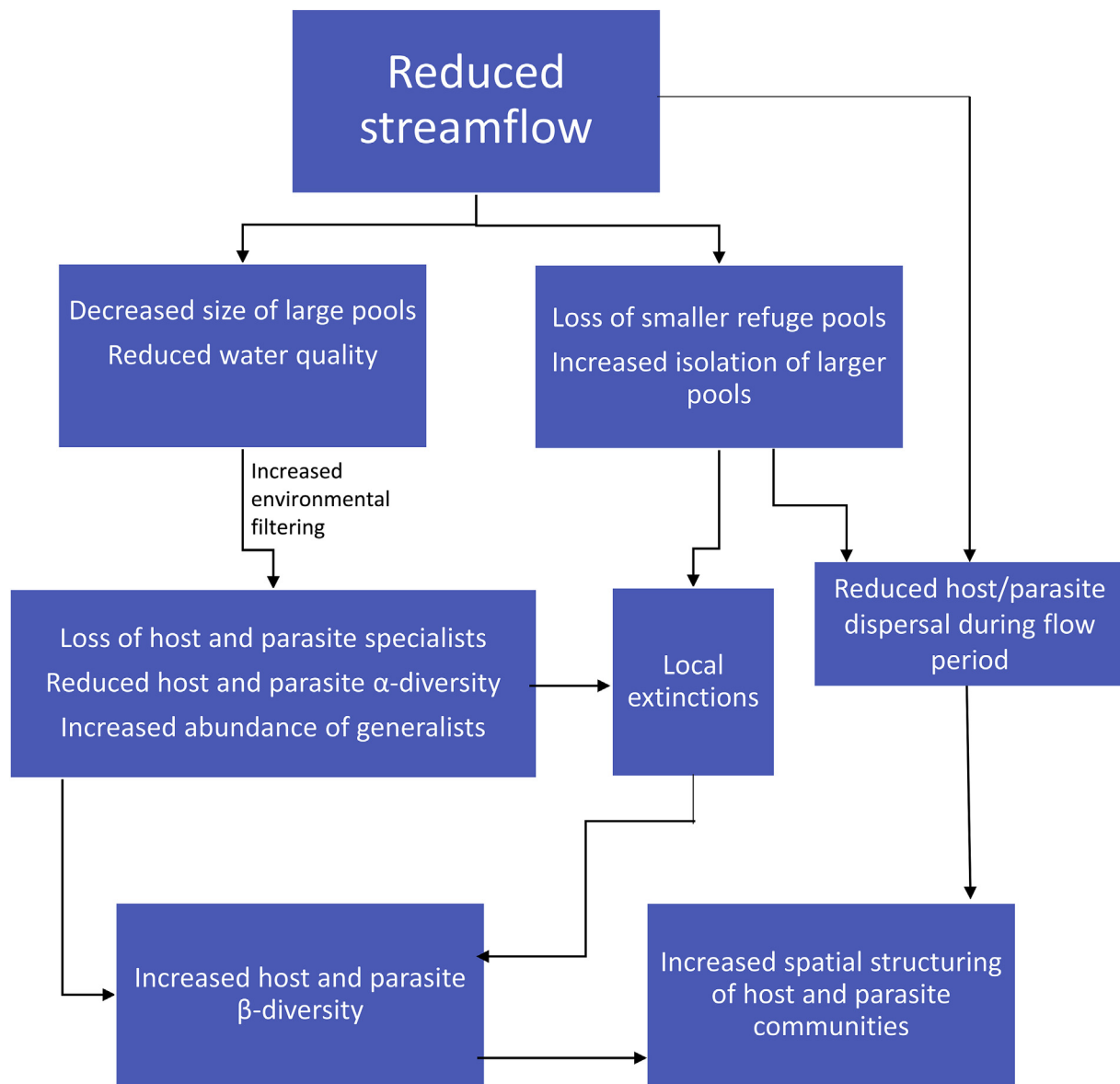


Fig. 2. Network of predicted changes in host and parasite communities in intermittent rivers as a consequence of decreased streamflow because of climate change.

assemblages of hosts and parasites (Jaeger et al., 2014). We predict that a reduction in streamflow as a result of climate change will lead to increased fragmentation of refuge pool habitats, local extinction of host and parasite species, a change in species composition to more generalist (often alien) hosts and parasites, and an increased structuring of host/parasite interactions along the length of the river (Fig. 2).

3.1. Climate change will reduce streamflow and increase habitat fragmentation

Streamflow is principally determined by the difference between precipitation and evapotranspiration (Milly et al., 2005). Over the last 50 years, climate change has had a major impact on precipitation and evapotranspiration, and therefore on the hydrology of freshwater ecosystems throughout the world, and particularly in arid, semi-arid and Mediterranean climatic regions. Mostly because of climate forcing, streamflow has decreased by more than 30% across large areas of southern Europe, the Middle East, western and southern Africa, southeast Asia and Australia, and by 10–30% in western North America and South America (Milliman et al., 2008; Dai et al., 2009). Projections from climate change models suggest that these decreases will continue

into the future; for global mean temperature rises of 2 °C above current levels, mean streamflow reductions (over a range of General Circulation Models and Global Hydrological Models) of up to 50% are predicted by 2050 for parts of Europe, the Middle East, southern Africa and Australia (Jiménez-Cisneros et al., 2014; Schewe et al., 2014). Changes in levels of precipitation and evapotranspiration are also likely to lead to more frequent and severe droughts, which will increase human demand for water resources, further exacerbating climate-forced reductions in streamflow (Jaeger et al., 2014).

Climate change is expected to increase the percentage of rivers and river reaches with intermittent, rather than perennial flow, and to increase the duration of no flow periods in existing intermittent rivers (Datry et al., 2018). This will reduce the number, size and connectivity of refuge pools, leading to increased habitat fragmentation, with potentially important consequences for free-living aquatic organisms and their parasite fauna. During the lentic phase, refuge pools gradually decrease in surface area and volume, with consequent increases in water temperature and solute concentrations, and decreases in dissolved oxygen (Datry et al., 2016b). Extended periods of no flow may therefore lead to complete drying of smaller refuge pools, with the loss of any aquatic fauna that have not evolved physiological tolerance to

sustained loss of water (Stubington and Datry, 2013; Ogston et al., 2016), while larger pools may decrease substantially in size, with concomitant increases in densities of aquatic fauna and deteriorating water quality (Magoulik and Kobza, 2003).

3.2. Increased habitat fragmentation will alter parasite abundance and species composition in refuge pools

Most studies of habitat fragmentation have focused on free-living mammals and birds in terrestrial (usually forested) landscapes, and have usually found a decrease in community richness and a change in community composition in fragmented habitats (Morris, 2010). The effects of fragmentation on parasite fauna and disease dynamics, however, are relatively poorly understood. Fragmentation has frequently been hypothesised to facilitate outbreaks of infectious disease (Suzán et al., 2012), but empirical studies have found variable effects on disease dynamics, often in similar host/parasite systems in different locations. Laurance et al. (2013), for example, found that fragmentation of rainforest habitat in northern Australia decreased the prevalence of blood-borne parasites (*Plasmodium* spp. and *Haemoproteus* spp.) in bird communities, while Pérez-Rodríguez et al. (2018) found a positive relationship between forest fragmentation and prevalence of these parasites in the Lesser Antillean bullfinch *Loxigilla noctis* in the Caribbean. Gottdenker et al. (2014) reviewed the effects of habitat fragmentation and other land use changes on the transmission of infectious diseases and found an increase in transmission in 57% of studies, while transmission decreased in 10% of studies, with either no change or a variable response in the remainder.

For aquatic parasites and their hosts, the consequences of increasing fragmentation of intermittent river systems will likely depend on parasite and host life history (see Fig. 2). The loss of small refuge pools should reduce parasite γ -diversity, although this may be mitigated to some extent by the positive relationship between pond size and diversity reported for both fishes (Dekar and Magoulik, 2007) and their parasites (Marcogliese and Cone, 1991). Nevertheless, the evidence (albeit preliminary) for lower parasite diversity in intermittent than in perennial rivers, provides more confidence for predicting that parasite species will be lost because of increasing habitat fragmentation. The decrease in parasite α -diversity and increase in β -diversity, which is presumed to be a normal feature of intermittent rivers during the lentic phase, should be intensified as increased fragmentation leads to more intensive environmental filtering.

Within refuge pools that survive the extended dry period, decreasing pool volume will increase the density of free-living fishes and invertebrates, which should initially increase the abundance of directly-transmitted parasites (although see the caveats regarding density-dependent transmission above). Although there have been few studies of fish parasitism in drying refuge pools, tadpoles of the treefrog *Hyla versicolor* had higher intensities of infection with a trematode (*Telorchis* sp.) in artificial ponds on a 49-day drying regime than in permanent ponds (Kiesecker and Skelly, 2001). Parasites with trophic transmission whose hosts survived initial environmental filtering would also be expected to increase in abundance because of increased predatory interactions. This may be particularly important for allogenic parasites which use piscivorous birds or mammals as definitive hosts, as terrestrial animals congregate at permanent pools during drought conditions (Lennox et al., 2019). Loss of host species through environmental filtering may also increase the abundance of parasites with frequency-dependent transmission, if more alternative host species have a dilution effect (Keasing et al., 2006).

Deteriorating water quality in refuge pools during an extended dry season (increasing water temperature and eutrophication, decreasing oxygen levels) will also influence parasite abundance. These effects are likely to be complex and species specific (see reviews in Marcogliese, 2001, 2016), but overall are likely to lead to an increasing prevalence and intensity of parasite infections because of direct effects on parasite

transmission or indirect effects on host immunocompetence. For example, increasing temperature within pools may increase parasite development rate and maturation time, leading to a rapid population expansion (Marcogliese, 2001). Eutrophication has been linked with increasing infection and greater pathology in a range of host/parasite systems, often due to increased densities of invertebrate intermediate hosts (McKenzie and Townsend, 2007; Johnson et al., 2010). Hypoxia has been associated with increased stress and reduced immune function in fishes, increasing rates of infection and parasite-associated mortality (Marcogliese, 2008; Whitney et al., 2016). If these conditions persist, then increasing host mortality should eventually lead to reduced parasite transmission and a decrease in infection pressure, although generalist parasites (those able to utilise a number of host species) may maintain large population sizes and push rarer host species, along with their specialist parasite fauna, to local extinction (McCallum and Dobson, 2002).

This intensified environmental filtering may lead to a dramatic change in species composition for both hosts and parasites in refuge pools, favouring hosts with broad environmental tolerances and parasites with broad host ranges. As a consequence, species assemblages in refuge pools may be increasingly dominated by invasive alien hosts, as these are typically environmental generalists (Ricciardi and Rasmussen, 1998; Devin and Beisel, 2007), and co-invading alien parasites, which are typically host generalists (Lymbery et al., 2014). Gagne and Blum (2016), for example, found an increase in prevalence and intensity of infection of the introduced nematode *Camallanus cotti* in native fish with declining rainfall and streamflow in Hawaii. This may lead to a nested community structure of both host and parasite species among refuge pools, with tolerant generalist species present at all sites, and more sensitive habitat and host specialists excluded from smaller pools which experience harsher conditions; such a nested pattern to increased β -diversity is a common feature of anthropogenic stress gradients (Gutiérrez-Cánovas et al., 2013).

3.3. Increasing diversity and reduced connectivity among refuge pools will lead to spatial structuring of host/parasite interactions

The ecological effects of greater rates of infection and increased host morbidity in refuge pools may last beyond the resumption of flow and a return to lotic conditions in the river. The long-term persistence and stability of community structure in intermittent rivers depends on dispersal during the lotic phase and recolonisation of previously isolated refuge pools (Sheldon et al., 2010). With fewer refuge pools surviving the dry season and a shorter period of river flow, connectivity among populations of fish and other aquatic organisms will be markedly reduced and this could be exacerbated by the effects of parasites on dispersal ability, as parasitic infection is known to reduce swimming speed and endurance of fishes (Whitney et al., 2016).

A decrease in connectivity should lead to greater spatial structuring of host/parasite interactions, with more interactions occurring within rather than among local communities of hosts and parasites. This may produce increased modularity in host/parasite interaction networks (Bordes et al., 2015), at least for those habitat and host specialists which are confined only to larger refuge pools. Small and isolated host populations are also more susceptible to demographic and genetic stochasticity, which may reduce genetic diversity and increase inbreeding, further increasing rates of infection (Suzán et al., 2012). The increased infection rates may create strong selection pressure on parasites for reduced virulence, which would enhance transmission by increasing host survival within refuge pools during lentic phases and improving swimming ability to allow dispersal among refuge pools when flow resumes.

4. Implications for conservation management

4.1. Conservation of freshwater fishes

Compared with the extensive reviews of disease emergence in terrestrial and marine ecosystems (e.g. Harvell et al., 2002; Lafferty et al., 2004; Ostfeld et al., 2008), the importance of parasitic disease as a driver of biodiversity loss in freshwater ecosystems has received surprisingly little attention (Okamura and Feist, 2011). Parasites are rarely considered when assessing threats to freshwater biota (Dudgeon et al., 2006), despite increasing reports of disease in freshwater fishes, amphibians and crustaceans (Johnson and Paull, 2011; Adlard et al., 2015). In intermittent river systems, there is currently a very poor understanding of the role of parasites in structuring communities of fish and other aquatic biota (Lennox et al., 2019), and infectious disease is typically ignored when developing strategies to manage the impacts of drought on freshwater fauna in intermittent rivers (e.g. Bond et al., 2015). Introduced alien parasites, in particular, may be very important in freshwater ecosystems, because invasive fishes are common in streams and rivers throughout the world (Okamura and Feist, 2011). Lymbery et al. (2014) found that of 98 published studies of co-introductions of alien host and parasite species, more than 50% of hosts were freshwater fishes. The Asian fish tapeworm, *Schyzocotyle (Bothriocephalus) acheilognathi*, for example, has been spread from northern Asia throughout the world, principally with imported common carp (*Cyprinus carpio*) and grass carp (*Ctenopharyngodon idella*), and poses a major threat to a number of endangered fish species (Hansen et al., 2006; Kuchta et al., 2018).

Infectious disease theory predicts that disease-induced host extinctions can occur as long as transmission does not follow a strict mass-action, density dependent form, or if parasites are not host-specific and can be maintained in reservoirs as the population of the endangered host declines (McCallum and Dobson, 2002; Best et al., 2012). While this is likely to lead to local extinctions of fish species in refuge pools of intermittent rivers, decreasing connectivity of refuge pools and increasing modularity of host/parasite interactions should slow parasite spread through the host metapopulation (Hess, 1996; Harding et al., 2012). This might be especially important for reducing the spread and impact of introduced parasites, although Stone et al. (2007) found that alien common carp (*Cyprinus carpio*), infected with co-invading *S. acheilognathi*, could disperse more than 250 km during episodic floods in the intermittent Little Colorado River in the USA. In addition, any benefits of decreased connectivity in slowing parasite spread must be balanced against the demographic dangers of local extinction and reduced recolonisation of refuge pools by fishes, and by increased stress and reduced genetic diversity in host populations, both of which may increase infection rates and disease severity (Gog et al., 2002; McCallum and Dobson, 2002). Heard et al. (2015) also found that increased connectivity in fragmented landscapes could sustain metapopulations of growling grass frog (*Litoria raniformis*) infected by chytrid

fungus (*Batrachochytrium dendrobatidis*), as long as host/parasite interactions were mediated by environmental heterogeneity (i.e. when environmental conditions prevented infection in some local populations).

4.2. Conservation of parasites

Although we typically view the conservation implications of parasitic disease through the lens of endangered hosts, there is now increasing recognition of the functional importance of parasites in all ecosystems and the need to ensure that they are considered in conservation planning (Gómez and Nichols, 2013; Dougherty et al., 2015; Carlson et al., 2017). Despite this, parasites are still extremely poorly represented in conservation assessments. For example, disregarding temporarily parasitic freshwater mussels, only two parasitic animals (*Hematopinus oliveri*, the pygmy hog louse, and *Hirudo medicinalis*, the medicinal leech) are included in the IUCN Red List of threatened species (IUCN, 2019), despite the fact that parasites have been estimated to account for at least one third of all the species on earth (Poulin, 2014). Clearly, a major paradigm shift is needed in the way that conservation practitioners and the general public view parasites if we are ever to move beyond the extreme bias in current conservation efforts towards free-living, charismatic vertebrates, and replace it with a more rational focus on the preservation of healthy, functioning ecosystems (Donaldson et al., 2016; Carlson et al., 2017).

While early studies on the effects of climate change on parasites suggested that global warming would be associated with range expansions and increases in disease outbreaks (Patz et al., 1996), recent work suggests a more nuanced view, with context-specific range shifts driven by the changes in temperature and a range of other climatic variables on both hosts and parasites (Lafferty, 2009; Marcogliese, 2016). For aquatic parasites in intermittent rivers, increasing habitat fragmentation as a result of climate change is likely to lead to declining population sizes and possible extinction, despite temporary increases in prevalence of some species as refuge pools contract in size. The parasite species at most risk of extinction will be those with high host specificity, density-dependent transmission or complex life cycles (Cizauskas et al., 2017; Thompson et al., 2018).

5. Conclusions

This review has raised far more questions than answers, because of the paucity of studies of aquatic parasites in intermittent river systems. Nevertheless, examining the ecology of intermittent rivers and the implications of this for disease transmission has provided some clear directions for further research and predictions about what this proposed research may find (Table 2). A consideration of the likely effects of climate change on intermittent rivers has also highlighted important management implications for the conservation of freshwater fishes and their native parasites. First, the likely increase in prevalence and severity of parasitic disease in dry season refuge pools means that disease-

Table 2
Suggested areas for future research on aquatic parasites in intermittent river systems.

Research area	Predictions
Compare parasite communities in intermittent and perennial rivers/reaches	1) Greater parasite diversity in perennial rivers/reaches 2) Parasite communities in intermittent rivers/reaches are a nested subset of those in perennial rivers/reaches
Compare parasite communities in refuge pools of different size Longitudinal study of parasite communities in refuge pools during no-flow period	Parasite communities in smaller pools are a nested subset of communities in larger pools 1) α -diversity and γ -diversity decrease, β -diversity increases over time 2) Specialist parasites and those with complex life cycles drive α -diversity loss over time 3) Generalist parasites and those with density-dependent transmission increase in prevalence over time
Compare parasite and host communities in rivers with different levels of intermittent flow Compare host/parasite interaction networks in rivers with different levels of intermittent flow	1) Greater intermittency favours generalist parasites and hosts 2) Greater intermittency favours alien parasites and hosts Greater intermittency favours increased network modularity

related mortality should be included in population models that are used to guide policy for water extraction and environmental flows in intermittent river systems. Second, the extinction risks to fish and parasite fauna that are associated with increased environmental filtering during lentic conditions and reduced dispersal during the lotic phase highlights the need to protect, restore or create new refuge pools in intermittent systems where streamflow is predicted to decline. Finally, an expected increasing domination of intermittent river communities by generalist species underscores the importance of control programs for alien hosts and parasites in a changing climate.

Declaration of competing interest

The authors have no conflicts of interest to declare.

Acknowledgements

Thanks to Ashley Lymbery for assistance with the references. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. The authors have no conflicts of interest to disclose.

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