

POLICY PERSPECTIVE

Don't move a mussel? Parasite and disease risk in conservation action

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Abstract

Freshwater mussels are one of the most endangered animal groups globally, making them a high conservation priority. Conservationists increasingly employ translocation or captive breeding procedures to support ailing populations, and the ecosystem engineering capabilities of mussels are being increasingly harnessed in bioremediation projects. However, there is little consideration of the risk of pathogen transmission when moving mussels from hatcheries or wild donor populations into new habitats. This is of significant concern as recent developments suggest parasites and diseases are highly prevalent and have contributed to several mass population-level die-offs. Here, we explicitly highlight the risks of pathogen spread in mussel translocations, explore how these risks are mediated, and provide recommendations for both research and action to avoid the inadvertent spread of virulent pathogens when conserving vulnerable mussel populations. While targeted at freshwater conservationists, this perspective has relevance for considering translocation-mediated disease and parasite spread in any study system.

KEYWORDS

captive breeding, freshwater, pathogen, prevalence, translocation, transmission, unionid

1 | INTRODUCTION

Freshwater mussels (order Unionida, henceforth referred to as “unionids”) are globally distributed ecosystem engineers, playing a key role in many lentic and lotic freshwater ecosystems. Along with recycling and storing nutrients, they create structural habitat, modify the substrate and food webs, and provide a range of intangible cultural services (Vaughn, 2018). However, unionids are also among the most endangered animal groups in the world; nearly 50% of species are threatened or near-threatened, rising to 70% in North America (Lopes-Lima et al., 2018). While

many threats (such as pollution or natural system modification) are recognized, there have also been enigmatic declines with less obvious causes (Haag, 2019), though disease has recently been proposed as a possible explanation (Carella et al., 2016; Richard et al., 2020).

The dire conservation status of unionids has spurred significant interest in captive breeding programs and translocations, to augment ailing populations, reintroduce mussels to an historic range or move them away from threats (Haag & Williams, 2014; Strayer et al., 2019). Bioremediation projects also involve moving large numbers of unionids to exploit their ecosystem engineering capabilities (Sicuro et al., 2020). However, translocations may

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also move parasites or diseases (collectively, “pathogens”), which can and has led to population- or species-level extinctions in other organisms (Daszak et al., 2000). Unionids host a range of pathogens (Grizzle & Brunner, 2009; Brian & Aldridge, 2019), though 88% of all European and North American mussels are predicted to be undersampled in terms of their endosymbionts, and the pathogenicity for many of these symbionts remains unknown (Brian & Aldridge, 2019). While we still lack substantial knowledge in this area, and use the term “pathogen” loosely to refer to any endosymbiont that may have a negative effect, many organisms have been shown to harm unionids (Table S1), and while pathogen spread as a result of mussel conservation actions is beginning to be discussed (e.g., Waller & Cope, 2019; Wolf et al., 2019), an explicit examination of risks and their mediators remains absent.

Some pathogens (e.g., bacteria, viruses, ciliates) complete their entire life cycle in mussels, and can transfer passively between mussels in the water column. Modern molecular techniques are revealing that these cryptic pathogens are much more common than previously realized (e.g., Carella et al., 2016; Goldberg et al., 2019; Richard et al., 2020). By bringing previously disparate populations together, translocations therefore may spread unrecognized disease agents through the landscape. Other pathogens (e.g., digenean trematodes, unionicolid mites, leeches) rely on a suite of intermediate and definitive hosts, leading to a diverse range of possible outcomes dependent on the ecosystem receiving the translocation. To ensure effective conservation, these outcomes and their associated risk factors must be clearly understood. In this perspective, we begin by outlining the scope of unionid translocations. We then define the associated pathogen-related risks, and provide research priorities and practical recommendations to ensure conservation actions do not unwittingly promote pathogen spread in vulnerable populations.

2 | SCOPE OF UNIONID TRANSLOCATIONS

We distinguish the source population (population from which mussels are taken) from the recipient population (existing population to which mussels are added) and the resultant population (total mussel population resulting from the translocation). In the case of captive breeding, the source and recipient populations can be the same.

A systematic literature review shows dramatic increases in both the numbers of papers reporting unionid translocations and the number of translocation events since the 1990s, with a recent tailing off attributable to a lag between a translocation and the publication reporting it (Figure 1a).

We also note that many translocations are not reported in the peer-reviewed literature (Haag & Williams, 2014), suggesting the total number is likely to be higher. Nearly 45% of all translocations were motivated by restoration (Figure 1b), though this was disproportionately driven by North American trends and motivation differed between continents ($\chi^2_{12} = 97.0, p < .001$); in Europe, more translocations were for experimental purposes (e.g., exploring growth rates in different environments). Whether or not mussels were already present in the recipient ecosystem differed with the purpose of the translocation (Figure 1c; $\chi^2_9 = 246, p < .001$), with restoration intuitively having the highest number of translocations where the recipient population had been extirpated. However, each purpose had at least 19% of translocations where there was an extant recipient population (overall mean 34%), and 35% did not report this information, leaving us unable to quantitatively assess the risk of pathogen spread. The incorporation of a pre-introduction quarantine varied with mussel presence in the recipient ecosystem ($\chi^2_6 = 108, p < .001$), with quarantine more likely when mussels were present (Figure 1d). However, in total only 34% of translocations involved a quarantine stage.

Our review suggests that vulnerable populations may be slightly less at risk from translocated pathogens than stable populations. As expected, the threat status of translocated species varied with purpose ($\chi^2_{15} = 236, p < .001$): restoration translocations (with a recipient population more commonly absent) involved the highest proportion of threatened unionids (47%), compared with experimental studies which generally used species categorized as Least Concern (Figure 1e). Where threatened species were translocated, the distance moved between source and recipient population was shorter (mean 48 km) than for stable species (mean = 125 km; $t_{199} = 4.11, p < .001$), potentially reducing the chance of pathogen transfer to immunologically naïve populations in these more vulnerable species (Figures 1f and 2c). However, this may be offset by the fact that significantly higher number of mussels were moved per translocation for the purposes of restoration (mean = 465) and conservation (mean = 2,597) than for biomonitoring (mean = 100) or experiments (mean = 58; $F_{3,407} = 19.88, p < .001$), and significantly more mussels were moved per translocation when there was an extant recipient population (mean = 438) than no recipient population (mean = 325, $F_{3,407} = 5.13, p < .01$). In addition, currently stable populations could undergo pathogen-driven declines in future (see Section 4), or act as an abundant reservoir for pathogens that could threaten more vulnerable populations or species.

Overall, translocations are common and widespread, though focused (in English-language literature) in North

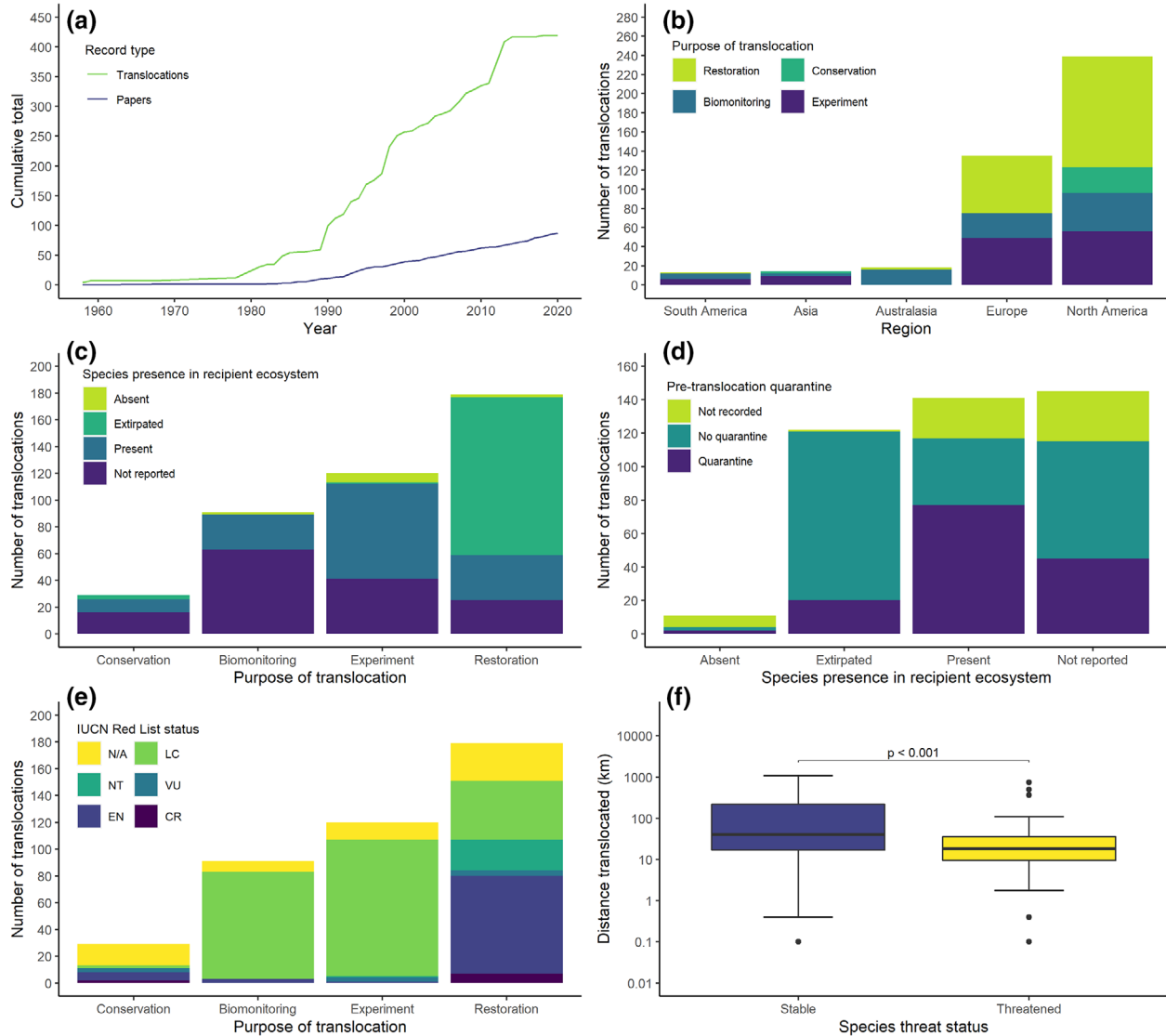


FIGURE 1 Results of a systematic search of the Web of Science database for literature describing unionid translocations. The dataset comprises 419 translocation events across 87 publications (see Supplementary Methods for protocol and screening criteria). (a) Cumulative increase in translocation events and publications reporting them. Subsequent graphs use individual translocation events, of which several were often reported in a single publication. (b) The geographic distribution of translocations stratified by broad purpose category. Categories are restoration (supplementing or reestablishing a population), conservation (translocating a population specifically under threat, often due to construction), biomonitoring (generally to assess ambient concentrations of heavy metals or other pollutants), and experiment (other research for information-gathering rather than conservation directly). (c) The current and historical presence of the translocated species in the recipient ecosystem across different translocation purposes. (d) Presence or absence of a pre-translocation quarantine stage, grouped by species presence in recipient ecosystem. (e) Threat status of translocated mussels (according to IUCN Red List) across translocation purposes. (f) Euclidean distance between source and recipient site, compared across stable (Red List status LC or NT) and threatened (VU, EN, or CR) species

America and Europe. This is particularly concerning given the high percentage of those translocations with extant recipient populations. There is significant scope for pathogen spread between source and recipient populations; in the following sections, we explore the factors determining this outcome, and the implications for already vulnerable populations.

3 | DETERMINING THE RISK OF PATHOGEN SPREAD

The risk of pathogen spread in translocations is determined by four key factors: pathogen prevalence, host population density, unionid immune capacity, and pathogen life-history (Figure 2). These factors have not been

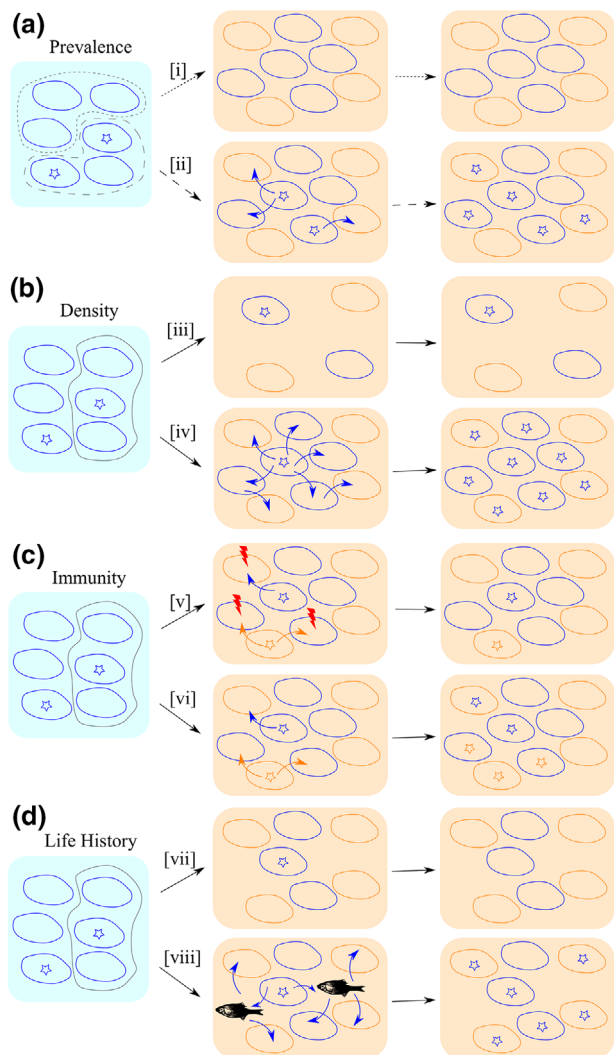


FIGURE 2 Determinants of risk when translocating individuals of a source population (blue mussels and boxes) to a recipient population (orange mussels and boxes), when pathogens originating in either the source (blue stars) or recipient (orange stars) population are involved. Colored arrows indicate pathogen spread. (a) Pathogen prevalence in the source population will determine the chances of translocating pathogen-free mussels [i] or infected mussels [ii], which can spread in the resultant population. (b) A low-density resultant population [iii] may prevent rapid pathogen spread, while spread could be facilitated by high densities [iv]. (c) Non-naïve recipient populations that already have pathogens may have immunological resources (red lightning bolts) and vice versa, thus mediating disease [v], while naïve recipient populations may stimulate an outbreak in the resultant population [vi]. (d) For multihost pathogens in the source population, if other obligate hosts are absent in the recipient ecosystem [vii] the pathogen cannot persist, but if those hosts are present, the pathogen can spread in the resultant population [viii]

considered for unionid mussels, so we use examples from other systems to illustrate their importance.

The first of these is prevalence: when taking mussels from the source population, the proportion of mussels infected (in addition to total number translocated) will determine the likelihood of transporting pathogens (Figures 2a and 3). For example, the North American invasive amphipod *Crangonyx pseudogracilis* hosts a microsporidian pathogen in approximately 10% of individuals in its native range. In its invaded range, the microsporidian is either present at near 100% prevalence (e.g., in the United Kingdom, the Netherlands, and France; Galbreath et al., 2010), or is completely absent (e.g., in Portugal; Banha et al., 2018). This may be because northern European invasive populations were established by an introduction of amphipods hosting this pathogen, while the Iberian population was established by pathogen-free amphipods (Banha et al., 2018). The median translocation in our review comprises 50 individuals; therefore, a pathogen present in just 5% of individuals has a 92% chance of being transported to the recipient population in at least one mussel (Figure 3). Given translocation sizes can often reach the thousands (e.g., Layzer & Scott, 2006), there is high scope for moving and spreading even low-abundance pathogens.

The second factor determining pathogen spread is the density of the resultant population (Figure 2b). Creating a population with low densities limits the spread of pathogens, while high-density populations facilitate rapid transmission. Density is an important mediator of pathogen dynamics in natural populations (e.g., Lafferty, 2004) and captive held organisms (Meeus et al., 2011). Therefore, unionid translocations and captive breeding programs, which artificially manipulate density, could stimulate previously cryptic or low-prevalence pathogens to spread rapidly.

Host immunity plays a well-documented role in disease mediation (Figure 2c). For example, an attempted translocation of endangered wolves in Yellowstone National Park failed due to immune naivety of the introduced wolves, which received parasites from local canines and experienced pack extinction (Almberg et al., 2012). Immune responses are poorly explored in unionids; though bivalves generally lack an adaptive immune system, they can mount an effective innate immune response against parasite attack (Munoz et al., 2006). Populations may be differentially adapted to pathogens, so understanding population connectivity and gene flow is key. This is particularly important if translocations involve moving endangered mussels between remnant populations that have been reproductively isolated for a long time.

Finally, the likelihood of pathogen spread is dependent on the pathogen's life history (Figure 2d). Pathogens

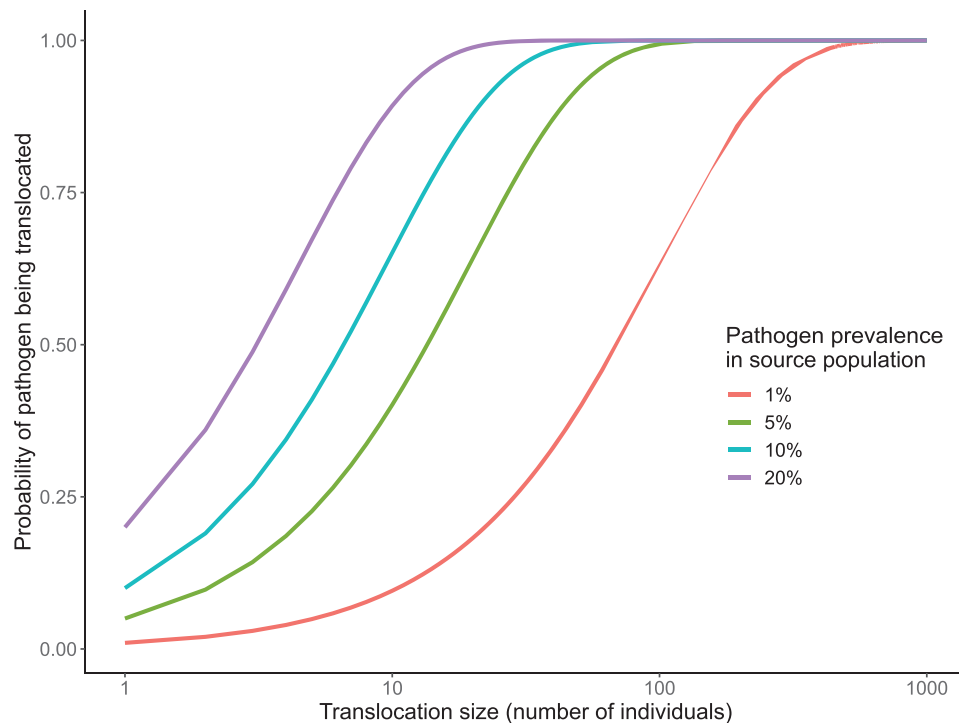


FIGURE 3 The probability of a pathogen being translocated from the source population along with a host mussel increases rapidly with translocation size and pathogen prevalence. Note log-transformed x-axis. Probabilities were calculated as $P(X \geq 1)$ (i.e., the probability of at least one translocated mussel being infected), where $X \sim \text{Binom}(n, p)$ with n representing the number of mussels translocated (1 to 1,000) and p representing pathogen prevalence (0.01, 0.05, 0.1 or 0.2)

requiring a single host (e.g., bacteria, viruses, ciliates) could persist in mussel populations regardless of wider species assemblages, while pathogens that require multiple hosts (e.g., digenean trematodes, some unionicolid mites and leeches) will not persist unless their other hosts are also present. Host species often determine pathogen distribution patterns (e.g., Paterson et al., 2019), suggesting an ecosystem-wide perspective is required.

While these determinants of risk have intuitive application for direct translocations (i.e., a mussel being moved from one location to another), they also apply to increasingly popular captive breeding programs (Figure 4). This process contains risks for source populations from which larval mussels are drawn (Figure 4c), for juvenile mussels both in the facilities and introduced to the recipient population (Figures 4e, g), and for the recipient population itself (Figure 4h); the likelihood of these occurrences is determined by the processes outlined in Figure 2. Due to close confinement and high densities, breeding facilities often act as reservoirs of disease, which is then spread wherever the organisms are distributed. For example, the spread of whirling disease in trout is almost exclusively driven by artificial rearing facilities (Bartholomew & Reno, 2002), and the vulnerability of multiple marine bivalves to *Vibrio* spp. bacteria leads to frequent outbreaks and spread in shellfish hatcheries (e.g., Elston et al., 2008).

4 | OUTCOMES OF RISK: CONSEQUENCES FOR POPULATIONS

We now consider the outcomes of these risks for unionid populations. Unionids possess a broad range of pathogenic fauna, including trematodes, mites, ciliates, nematodes, bacteria, and viruses (Brian & Aldridge, 2019; Table S1). There is also indirect evidence for parasitism by other taxa such as glossiphoniid leeches (Bolotov et al., 2019), highlighting the need for continued research in this area. Many pathogens have deleterious effects on unionid populations, including castration by bucephalid trematodes, and recent evidence of virally driven mass mortality (Table S1). These pathogens may be shared between populations, depending on whether the pathogen is in the source population, recipient population, or both. Table 1 explores these potential outcomes and how they are mediated. Parasite prevalence emerges as a near-ubiquitous influence on the likelihood of pathogen sharing. Other risks depend on the type of pathogen considered: pathogens requiring multiple hosts may be less affected by the density of the resultant population as transmission is mediated by other host species, while the opposite is true for single-host pathogens. Further, Table 1 only considers outcomes for a *single* pathogen. However, mussels host

TABLE 1 Possible outcomes of pathogen (including virus, bacteria and macroparasite) spread caused by translocation actions, where source population refers to the population that mussels are being removed from, recipient population refers to the existing population that translocated mussels are being added to, and the resultant population is the total mussel population resulting from the translocation. For simplicity, this table considers a single pathogen. (a) Major determinants of risk for pathogen spread, depending on whether the pathogen is present in the source population or the recipient population. (b) Possible outcomes of translocation with respect to pathogen spread. The first two columns specify whether the source and recipient populations respectively have a single-host pathogen (SHP; i.e., a pathogen that does not require another host in the life cycle), a multihost pathogen (MHP) or no pathogens (NP) prior to translocation

(a)			
Origin of pathogen	Determinant of risk	Corresponding figure	Risk type
I: Source population	Prevalence in source pop	1a	1
	Vulnerability in recipient pop (i.e., immune naivety)	1c	2
	Presence and density of other hosts in pathogen life cycle in recipient ecosystem	1d	3
II: Recipient population	Vulnerability in source population (e.g., immune naivety)	1c	4
III: Either	Density of resultant population	1b	5
(b)			
Source population	Recipient population	Possible outcome	Risks affecting outcome
SHP	No mussels	SHP to resultant pop	1
	NP	SHP outbreak in recipient pop	1, 2, 5
	SHP	SHP outbreak in resultant pop	5
MHP	MHP	Both MHP and SHP in resultant pop	1, 2, 4
	No mussels	MHP to resultant pop	1, 3
	NP	MHP outbreak in recipient pop	1, 2, 3
NP	SHP	Both MHP and SHP in resultant pop	1, 2, 3, 4
	MHP	MHP outbreak in resultant pop	3
	No mussels	No pathogen-associated risk	N/A
NP	NP	No pathogen-associated risk	N/A
	SHP	SHP outbreak in translocated source-pop mussels	4, 5
	MHP	MHP outbreak in translocated source-pop mussels	3, 4

multiple macro- and microparasites simultaneously (Brian & Aldridge, 2021b; Richard et al., 2020), leading to a complex set of possible interactions. Consider again a median translocation size of 50 from a mussel population that now has two pathogens, both at a conservative 5% prevalence. Assuming they occur independently, the likelihood of at least one of those pathogens being translocated rises to 99.4%, a near-certainty. We suggest cryptic movement of pathogens is exceedingly common in freshwater mussel translocations.

In extreme cases, pathogens may lead to population collapse in bivalves (Katsanevakis et al., 2019; Richard et al., 2020). However, pathogens can significantly affect ecosystems even without complete collapse. Pathogens interact with other sublethal stressors to greatly enhance unionid mortality; for example, *Anodonta anatina* infected with the castrating trematode *Rhipidocotyle fennica* suffered significantly higher mortality than noninfected mussels in both anoxic and food-depleted environments, an effect not observed under normal environmental conditions (Jokela

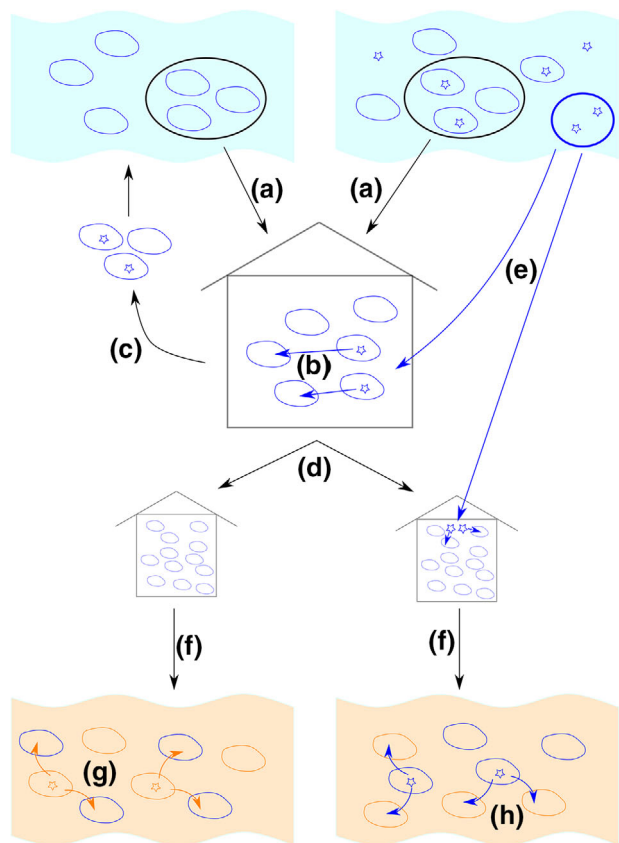


FIGURE 4 Pathogen-associated risks when moving captive-bred mussels. Buildings represent breeding facilities, black arrows indicate movement of mussels and colored arrows represent pathogen spread. Mussels, environments, and pathogens are colored according to Figure 2. Adult mussels may be collected from environments with or without pathogens to harvest glochidia (larval mussels brooded by the female) (a); if they are held in shared tanks or equipment is improperly cleaned, pathogens may spread between populations (b) and then transported back into previously unaffected populations via returning the adult mussels (c) sampled in the first step. In the process of both holding adults (a) and growing juveniles (d), water from source environments is frequently used, which may contain transmission stages of pathogens (e) and infect mussels. When mussels are placed in the environment after captive breeding (f), they may be naïve and suffer high infection rates from pathogens in the recipient environment (g), or contain pathogens themselves which may spread to vulnerable mussels in the recipient population (h). The likelihood of stages a, b, e, g, and h will depend on the processes outlined in Figure 2

et al., 2005). Further, changing environmental conditions may stimulate a sudden outbreak. *Perkinsus marinus* was repeatedly introduced into various oyster populations where it remained undetected until it was stimulated to proliferate into an epizootic by extreme warming (Ford, 1996). Environmental extremes are increasingly common, and may be related to die-offs of mussel fauna in recent decades (Strayer et al., 2019). Pathogens may also inter-

act to worsen outcomes for vulnerable species. The Clinch River population of the unionid *Actinonaias pectorosa* suffered a mass die-off in 2016 hypothesized to be pathogen-related. Before the die-off, the prevalence of castrating parasites was 12.5%; after the die-off it was 90% (Henley et al., 2019). Whether or not the castrators contributed to the die-off, their high subsequent prevalence significantly limits the capacity of the population to recover.

Overall, we believe such environment–pathogen or pathogen–pathogen interactions may become increasingly common as pathogen spread may be amplified by both translocation actions and environmental extremes. It is therefore crucial to limit their spread and carefully consider their role in conservation actions.

5 | RECOMMENDATIONS

In this section, we provide explicit policy recommendations, focused on two key areas: Research Recommendations (RR), and Action Recommendations (AR).

RR1: Understand parasite diversity and prevalence in both source and recipient populations.

The most important first step is to identify possible pathogens from a wide range of species and regions, and determine their pathogenicity. Over 85% of North American and European mussel species are considered undersampled in terms of their pathogen fauna (Brian & Aldridge, 2019), and our poor understanding of mussel pathogens is a key reason why many translocated mussels are not screened for diseases (Haag & Williams, 2014). Different pathogens are found in different populations (e.g., Chittick et al., 2001); translocations should ensure they are not spreading pathogens to new locations, which requires understanding pathogen geography and diversity. Within-population variation is also important: differences in filtering behaviour or sizes of individuals can influence parasite communities (Brian & Aldridge, 2021b). Assessing these factors may be difficult for endangered species, but recently developed nondestructive methods may help (e.g., Brian & Aldridge, 2021a).

RR2: Understand pathogen life histories.

This important determinant of risk has three key facets: how the pathogen responds to different host densities, how biotic and abiotic aspects of the habitat influence pathogen spread, and how pathogen exposure varies temporally (Brian & Aldridge, 2021b). This is particularly important when mussels cannot be screened for pathogens extensively: if we know how a pathogen spreads, or what times of year are important in its life-history, we can better

predict the risk of it successfully establishing somewhere new, and how risk varies among scenarios. For example, translocating mussels upstream in the same catchment area may pose a greater risk of infecting recipient populations than moving mussels downstream, where transmission stages are more likely to have travelled anyway. These factors will vary from pathogen to pathogen, precluding generalities and necessitating further study.

RR3: Understand immune responses of unionid mussels.

Very few published studies on unionid immune responses exist: this area should be explored further. The general principles we have discussed apply whether one considers pathogen transfer between the same species or different species. However, population- or species-specific immune adaptations may significantly influence the success of pathogen communities, and assessing variable resistance or tolerance to infection is an important part of understanding the risks of translocation. Additionally, RR2 and RR3 together will help in determining the dangers of pathogen spread for different translocation distances (Figure 1f).

ARI: Only translocate when absolutely necessary.

This is not a novel recommendation (see Patterson et al., 2018; Strayer et al., 2019), as it is widely accepted that translocation is not a substitute for addressing the causes of decline. However, we bring a new context to this, especially given the high number of experimental translocations that have recipient populations (Figures 1b, c). While experimental translocations are often useful to understand unionid biology, they should consider the risk of transporting pathogens to naïve populations. Regardless of purpose, poorly considered translocations contain significant scope for pathogen spread (Table 1), and may exacerbate rather than alleviate the significant threat to endangered populations. This is particularly pertinent as it appears that vulnerable populations (which are likely translocation targets, either as a source or recipient populations) after die-offs have high pathogen prevalence, which may have contributed to the die-off (Henley et al., 2019).

AR2: Quarantine translocated mussels, but tailor this to the pathogen of concern.

Quarantine procedures are well-established for avoiding the spread of zebra mussels (Patterson et al., 2018), but little consideration has been given to avoiding endoparasites or disease spread. These should be informed by RR1, to identify the possible pathogens of concern. For example, macroparasites such as trematodes and mites may require

a long quarantine, to allow for life-history stages of these organisms to emerge as evidence of infection. However, bacterial or viral infections may remain cryptic; while a short quarantine would allow for nondestructive tissue assessment and identification of potentially infected mussels, a long quarantine could facilitate their spread among mussels held together. Treating water in quarantine facilities with UV light may be effective at stopping bacterial or viral spread through the water (Schneider et al., 2009), but this cannot penetrate shells and kill pathogens *in situ*.

AR3: Where possible, consider introducing mussels as glochidia encysted on fishes.

The small size of glochidia (larval mussels) represents a significant barrier to vertical transmission, and to our knowledge, they have no recorded pathogens, though this has not been studied in detail. This recommendation will not apply in some scenarios (e.g., moving an adult population faced with environmental degradation), but is an option for captive breeding programs, or for supplementing existing populations, though it does make assessing translocation success difficult. This strategy should carefully consider the risk of spreading pathogens of fish hosts (the vectors for glochidia), though this aspect has been evaluated elsewhere (e.g., Patterson et al., 2018). In addition, such a strategy will need to ensure pathogens are not extracted from the female mussel's gills along with the glochidia.

6 | CONCLUSION

Understanding pathogen risk is a key factor in taking successful conservation action (Gross et al., 2000). In this policy perspective, we have demonstrated the scope of unionid translocations and explored the possible risks of pathogen spread between already highly threatened populations and species. Importantly, cryptic pathogens exist in mussel populations, the effects of which can be stimulated and exacerbated by environmental variation. Translocations, if not carefully considered, have immense scope to promote the spread of these pathogens. We acknowledge that our recommendations represent ideal best practice; however, we see them, and this perspective, as a key starting point in considering pathogens when acting to conserve unionid mussels.

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DATA AVAILABILITY STATEMENT


All data supporting the review of unionid translocations, in addition to Supplementary Methods and Table S1, are available as supplementary material.

AUTHOR CONTRIBUTIONS

JIB and DCA conceived the idea. JIB and ISO collated literature, produced figures and tables, and drafted the manuscript. All authors contributed substantially to revisions.

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SUPPORTING INFORMATION

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

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