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Zoochorous dispersal of freshwater bivalves: an overlooked vector in biological invasions?

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Abstract – Vectors that underpin the natural dispersal of invasive alien species are frequently unknown. In particular, the passive dispersal (zoochory) of one organism (or propagule) by another, usually more mobile animal, remains poorly understood. Field observations of the adherence of invasive freshwater bivalves to other organisms have prompted us to assess the importance of zoochory in the spread of three prolific invaders: zebra mussel *Dreissena polymorpha*; quagga mussel *Dreissena bugensis*; and Asian clam *Corbicula fluminea*. An extensive, systematic search of the literature was conducted across multiple on-line scientific databases using various search terms and associated synonyms. In total, only five publications fully satisfied the search criteria. It appears that some fish species can internally transport viable adult *D. polymorpha* and *C. fluminea* specimens. Additionally, literature indicates that veligers and juvenile *D. polymorpha* can adhere to the external surfaces of waterbirds. Overall, literature suggests that zoochorous dispersal of invasive bivalves is possible, but likely a rare occurrence. However, even the establishment of a few individuals (or a single self-fertilising *C. fluminea* specimen) can, over-time, result in a substantial population. Here, we highlight knowledge gaps, identify realistic opportunities for data collection, and suggest management protocols to mitigate the spread of invasive alien species.

Keywords: ectozoochory / endozoochory / freshwater ecosystems / ichthyochory / invasive alien / secondary spread

Résumé – Zoochorie de bivalves d'eau douce ; un vecteur négligé dans les invasions biologiques ?
Les vecteurs qui sous-tendent la dispersion naturelle des espèces exotiques envahissantes sont souvent inconnus. En particulier, la dispersion passive (zoochorie) d'un organisme (ou propagule) par un autre, habituellement plus mobile, reste mal comprise. Les observations sur le terrain de l'adhésion des bivalves d'eau douce envahissants à d'autres organismes nous ont incité à évaluer l'importance de la zoochorie dans la propagation de trois envahisseurs prolifiques : la moule zébrée *Dreissena polymorpha* ; Moule Quagga *Dreissena bugensis* ; et la palourde asiatique *Corbicula fluminea*. Une recherche approfondie et systématique de la littérature a été menée dans de multiples bases de données scientifiques en ligne utilisant différents termes de recherche et synonymes associés. Au total, seulement cinq publications ont pleinement satisfait les critères de recherche. Il semble que certaines espèces de poissons puissent transporter intérieurement des spécimens adultes viables de *D. polymorpha* et *C. fluminea*. En outre, la littérature indique que les véligères et les *D. polymorpha* juvéniles peuvent adhérer aux surfaces externes des oiseaux d'eau. Dans l'ensemble, la littérature suggère que la dispersion par zoochorie des bivalves invasifs est possible, mais probablement une occurrence rare. Cependant, même l'établissement de quelques individus (ou un seul spécimen autofécondant de *C. fluminea*) peut, au fil du temps, entraîner une population importante. Ici, nous mettons en évidence les lacunes en matière de connaissances, identifions des opportunités réalistes pour la collecte de données et proposons des protocoles de gestion pour atténuer la propagation d'espèces exotiques envahissantes.

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Mots-clés : ectozoochorie / endozoochorie / écosystèmes d'eau douce / ichthychorie / espèce exotique invasive / propagation secondaire

1 Introduction

The majority of primary introductions of invasive alien species (IAS) are considered to have occurred via anthropogenic means (Hulme *et al.*, 2008; Solarz *et al.*, 2017). However, the natural (or 'unaided by humans') dispersal of organisms can also result in the arrival of an IAS in a new region (Hulme *et al.*, 2016). More importantly, the secondary spread of IAS from an established source population can often be facilitated by natural dispersal vectors, including water currents (hydrochory), wind (anemochory), and other animals (zoochory) (Bilton *et al.*, 2001; Hulme *et al.*, 2008; Coughlan *et al.*, 2017b). Recent European Union (EU) and United States of America (USA) legislation (EU Regulation 1143/2014 and Safeguarding the Nation from the Impacts of Invasive Species – amendment to Executive Order 13112, respectively) seek to prevent, control and eradicate IAS within both territories. In order to develop comprehensive IAS prevention and control measures, species risk assessments must consider not only broad invasion pathway categories, but also specific vectors (Essl *et al.*, 2015). Currently, however, our understanding of the natural dispersal processes operating between hydrologically unconnected water bodies remains limited (Soomers *et al.*, 2013; Incagnone *et al.*, 2015; Coughlan *et al.*, 2017a).

Zoochorous transport of one organism by another more mobile animal can facilitate dispersal of various taxa (see Fig. 1) (Reynolds *et al.*, 2015; Green, 2016; Coughlan *et al.*, 2017a). Many organisms, particularly propagule stages (*e.g.*, seeds, spores, eggs, ephippia, gemmules, statoblasts, or cysts) can be transported both internally, via the gastrointestinal tract (gut), or upon the exterior surfaces of other animals. The association where one organism (or propagule) is externally transported by another organism is categorised under various biological relationships which include, *inter alia*, ectozoochory, phoresis, commensalism, and fouling. Ectozoochory (synonyms epizoochory, exozoochory), a term originally used to describe the dispersal of plant propagules via external adherence to animal vectors, is now widely employed to refer to external dispersal of a variety of taxa (Reynolds *et al.*, 2015; Green, 2016; Coughlan *et al.*, 2017a). Endozoochory, a term originally used to describe seed dispersal, now encompasses the internal dispersal of a variety of taxa.

The spread of invasive alien bivalves represents a major threat to the function and biodiversity of freshwater ecosystems worldwide (Strayer *et al.*, 1999; Sousa *et al.*, 2009; Higgins and Vander Zanden, 2010; Douda *et al.*, 2017). In particular, zebra mussel *Dreissena polymorpha* (Pallas, 1771), quagga mussel, *Dreissena bugensis* (Andrusov, 1897) and Asian clam *Corbicula fluminea* (Müller, 1774) are prolific invaders, whose presence can have damaging ecological and economic consequences for invaded habitats (Pimentel *et al.*, 2005; Sousa *et al.*, 2014; Karatayev *et al.*, 2015). Moreover, despite management efforts to reduce invader spread within EU and USA territories, further range expansion of these bivalves has been observed (*e.g.*, Aldridge *et al.*, 2014; Benson, 2014; Caffrey *et al.*, 2016). Under optimal conditions, these bivalve species display rapid growth and high levels of fecundity, and can potentially form flourishing populations from a few founder specimens, or in the cases of *C. fluminea*, from even one self-fertilising individual (McMahon, 2002). In contrast to many freshwater bivalve species, the life cycles of these invaders do not include a parasitic larval stages (Mackie, 1991). Rather, planktonic larval (*e.g.*, veliger) stages can freely swim within the water column until settlement of the post-veliger (*e.g.*, juvenile) stages occurs. Both up-stream and between catchment dispersal of these bivalves has been predominantly attributed to anthropogenic activities, particularly by recreational water users (*e.g.*, anglers, boaters, and canoeists) (Kappes and Haase, 2012; Banha *et al.*, 2016). Nevertheless, possible alternative natural vectors of passive dispersal remain under-researched, even though these vectors may facilitate greater levels of invasive bivalve dispersal than is assumed (Johnson and Carlton, 1996; Kappes and Haase, 2012; Banha *et al.*, 2016). Field observations of *D. polymorpha* attachment to more mobile freshwater organisms (see Fig. 2) have prompted us to assess the importance of zoochory in the spread of invasive freshwater bivalves. Here, we examine the available literature concerning zoochorous dispersal of invasive freshwater bivalves: *D. polymorpha*; *D. bugensis*; and *C. fluminea*.

2 Methods

We systematically searched for relevant material using the on-line scientific databases Thomson-Reuters *Web of Science* and *Scopus*. An additional search for relevant material was preformed using *Google* and *Google Scholar*. All searches were undertaken in December 2016, and focused on various terms used in the literature. For example, the principle search term used to derive relevant material was: (mussel OR clam OR bivalv* OR dreissena OR corbicula) AND (external OR internal OR passive OR vector OR foul* OR *zoochorous OR *chory OR *zoon OR phor* OR gut OR *intestinal) AND (dispersal OR dispersion). Species scientific names (*D. polymorpha*, *D. bugensis* and *C. fluminea*) and common names were also used as search terms. Associated synonyms of search terms (*e.g.*, epizoon, entozoon, ectozoochory, endozoochory, passive dispersal, fouling, phoresy) were further used to assess and reduce the number of generated documents. Moreover, reference lists from all retrieved books and articles were screened for other relevant publications. Selected literature was then appraised for inclusion within this paper based upon pertinence to the core topic, *e.g.*, studies which directly evaluate zoochorous mediated dispersal of *D. polymorpha*, *D. bugensis* or *C. fluminea*. There was no restriction on publication year.

3 Results and discussion

The search yielded 219 and 161 publications from *Web of Science* and *Scopus*, respectively. *Google* and *Google Scholar* did not provide any additional pertinent material, within the

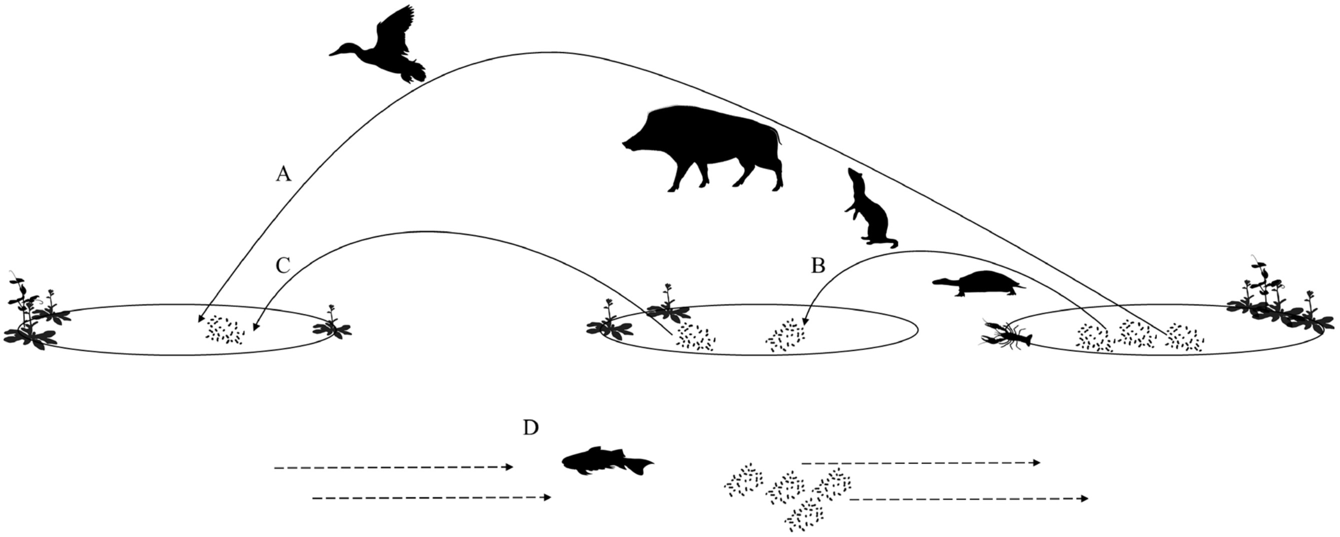

Fig. 1. Overland long distance dispersal (LDD) (A), short distance dispersal (SDD) (B), and ‘stepping stone’ dispersal (C) of invasive bivalve species (dot clusters) between isolated (*e.g.*, hydrologically unconnected) freshwater sites *via* possible zoochorous vectors. Equally, when sites are hydrologically connected (D) (*e.g.*, streams) additional aquatic vectors, such as fish species, may facilitate LDD, SDD or stepping stone dispersal. Moreover, zoochorous vectors may intensify invader spread across large aquatic areas (*e.g.*, large lakes). Dashed lines indicate water current.

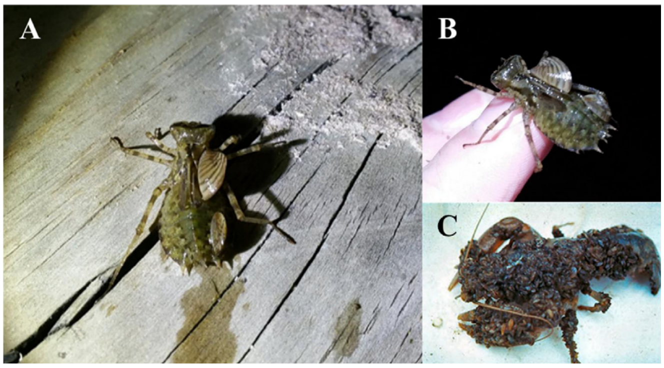

Fig. 2. (A & B) Two adult zebra mussels *Dreissena polymorpha* attached to the dorsal carapace of an odonata nymph *Epicordulia* sp. (Corduliidae) larva. The nymph was collected on Lake Mendota, Madison, WI (43°04′38.8″N 89°24′10.6″W) on 24th October 2016 *via* a minnow trap in 2 m of water (Photo credits, A.L. Stevens). The criteria used to identify species are described by Bouchard *et al.* (2004). (C) Adult crayfish specimen extensively fouled by *D. polymorpha* (Photo credit, Minnesota Department of Natural Resources).

first ten search-pages. Numerous studies suggested zoochory as a potential dispersal mechanism for various freshwater bivalves and other Mollusca species, however, many did not reference a citation for this assumption. Studies selected for inclusion within this paper are those which attempted to experimentally examine zoochorous dispersal of *D. polymorpha*, *D. bugensis*, or *C. fluminea*. In total, only five publications met the full search criteria (Tab. 1).

3.1 Endozoochorous dispersal

Many studies have reported the consumption of invasive bivalves by fish and bird species (*e.g.*, Robinson and Wellborn, 1988; Hamilton and Davison Ankney, 1994; Tucker*et al.*, 1996). In most cases, gut contents or faecal samples appear to suggest that the consumer can effectively digest *D. polymorpha*, *D. bugensis* and *C. fluminea* leaving only shell fragments (*e.g.*, Hamilton and Davison Ankney, 1994; Tucker*et al.*, 1996; Perello*et al.*, 2015). However, most studies do not examine endozoochorous dispersal and, therefore, do not attempt to assess the survival and viability of intact specimens (if any) found within retrieved gut or faecal samples. Equally, a variety of freshwater mollusca, such as pea clams (Sphaeriidae), valve snails (Valvatidae), pond snails (Lymnaeidae) and mussels (Mytilidae), have been shown to survive gut passage through different fish and waterbird species, albeit to various extents (Mackie, 1979; Brown, 2007; Belz *et al.*, 2012; van Leeuwen *et al.*, 2012).

Literature reviewed here (and many fish and waterbird dietary studies) indicate (or imply) that *D. polymorpha*, *D. bugensis*, and *C. fluminea* will not usually survive gut passage. Remarkably, Gatlin *et al.* (2013) recorded the survival of *C. fluminea* and *D. polymorpha* that have passed through the gut of migratory blue catfish (*Ictalurus furcatus*), a species which travels up to 689 km in a year (Tripp *et al.*, 2011). However, any intact bivalve specimens are more likely to be ejected over much shorter distances as dictated by gut retention times. Moreover, Gatlin *et al.* (2013) noted that these bivalves appear unable to survive gut passage through *I. furcatus* in waters above 21.1 °C, however, this is unlikely to overly inhibit dispersal potential as migrations typically occur when water temperatures are between 8 and 18 °C. Incidentally, we hypothesise that the observed increase in bivalve mortality may be due to greater host metabolic activity, as warmer water temperatures may increase digestion efficiency of some fish species (Mizanur *et al.*, 2014; De *et al.*, 2016). Conversely, higher water temperature can also result in reduced retention times within the gastrointestinal tract (De *et al.*, 2016).

The feeding ecology of fish and waterbird species, and associated digestive morphological traits, will likely influence

Table 1. Studies addressing zoochorus dispersal of zebra mussel *Dreissena polymorpha*, quagga mussel, *Dreissena bugensis* and Asian clam *Corbicula fluminea*. The bivalve species examined, method of investigation used, and a summary of findings are identified.

Reference	Species	Method	Summary of findings
Endozoochory			
Thompson and Sparks (1977)	*Corbicula fluminea*	Faecal sample collection	Live *C. fluminea* feed to lesser scaup ducks (*Aythya affinis*) did not survive gut passage.
Johnson and Carlton (1996)	*Dreissena polymorpha*	Faecal sample collection	Faecal samples recovered from mallard ducks (*Anas platyrhynchos*), which consumed juvenile mussels or concentrated suspensions of veligers, did not contain any viable specimens.
Gatlin *et al.* (2013)	*Corbicula fluminea* *Dreissena polymorpha*	Faecal sample collection	Twelve percent of *D. polymorpha* and 39 % of *C. fluminea* consumed in cool water (<21.1 °C) survived gut passage through migratory blue catfish (*Ictalurus furcatus*).
Mack and Andraso (2015)	*Dreissena bugensis* *Dreissena polymorpha*	Faecal sample collection	No dreissenids survived passage through the gut of round goby (*Neogobius melanostomus*).
Ectozoochory			
Johnson and Carlton (1996)	*Dreissena polymorpha*	Experimental attachment	Veligers and juvenile *D. polymorpha* transported (2.5 m) between ponds by walking mallard ducks, <0.5 mussel per trip.
Banha *et al.* (2016)	*Dreissena polymorpha*	Experimental attachment	Larvae of *D. polymorpha* can adhere and remain attached to a mallard duck carcass during simulated swims ($\leq 0.5\,\mathrm{m\,s^{-1}}$) and flights ($75\,\mathrm{km\,h^{-1}}$).

success of endozoochorous dispersal. Vector species that are acclimated to a diet containing bivalves are less likely to facilitate transport than individuals or species which are not. For example, Mack and Andraso (2015) documented no survival of dreissenids after gut passage through the round goby (*Neogobius melanostomus*). Previously, however, Andraso *et al.* (2011) had noted that mature *N. melanostomus* specimens can develop molariform teeth typical of those found in molluscivorous fish to prey on dreissenid mussels. Age, genetic and environmental factors are suggested to influence pharyngeal remodelling. Moreover, Index of Relative Importance analysis of *N. melanostomus* gut contents indicate a diet selective of veliger and juvenile dreissenid mussels (Thompson and Simon, 2014). In contrast, *I. furcatus* appears to be preferentially more piscivorous, although it is often described as an omnivorous opportunistic feeder (MacAvoy *et al.*, 2000; Aguilar *et al.*, 2016). Therefore, *ceteris paribus*, the digestion of bivalves by *I. furcatus* may be less efficient than digestion by adult *N. melanostomus*.

Many waterbird species are also known to consume bivalves (Piersma *et al.*, 1993; Hamilton and Davison Ankney, 1994). Thompson and Sparks (1977) observed that lesser scaup ducks (*Aythya affinis*) digested *C. fluminea* completely. However, *A. affinis* is a preferential rather than opportunistic consumer of macroinvertebrates (Gurney *et al.*, 2017). Within phylogenetic or ecological constraints, the avian digestive tract can respond to variable diet composition and quality by changing morphology and/or activities of digestive enzymes (Piersma *et al.*, 1993; van Gils *et al.*, 2003; Kohl *et al.*, 2017). Therefore, we argue that prior to acclimation of the gastrointestinal tract to the presence of bivalves within their diet, some waterbirds may facilitate endozoochorous dispersal. In support of such an argument, van Leeuwen *et al.* (2012) retrieved greater numbers of intact aquatic snail species from faecal samples obtained from smaller mallard ducks compared to larger individuals. This was surmised to reflect shorter retention times by smaller ducks, given that gut length and gizzard size are generally correlated to body mass. Accordingly, snails likely experienced less exposure to both gastric enzymes and abrasive mechanical digestion by the avian gizzard.

It appears that the thermal shock of sudden exposure to the high internal body temperatures of waterbirds (42 °C), and possibly hypoxia, can induce high mortality of *C. fluminea*, which generally does not tolerate water temperatures above 38 °C (McMahon, 1979; Lucy *et al.*, 2012). Similarly, the upper thermal limit of *D. bugensis* is likely between 25 and 36 °C (Spidle *et al.*, 1995). However, warm water (>15 °C) acclimated *D. polymorpha* can survive water temperatures up to 40 °C for between 20 and 75 minutes, depending on the rate of temperature increase (McMahon and Ussery, 1995; Spidle *et al.*, 1995; Beyer *et al.*, 2011) and therefore, may survive rapid passage through the avian gut if exposed to minimal abrasive damage. Accordingly, both fish and waterbird consumer species which are not acclimated to the presence of bivalves within their diet may potentially facilitate a dispersal event.

3.2 Ectozoochorous dispersal

Several publications cited anecdotal accounts detailing ectozoochorous dispersal of various bivalve species (see Rees (1965) for a collection of these accounts), no anecdotes concerning the ectozoochorous dispersal of *D. polymorpha*, *D. bugensis* or *C. fluminea* were found. However, Johnson and Carlton (1996) observed that walking mallard ducks (*Anas platyrhynchos*) could transport larvae and juvenile *D. polymorpha* a distance of 2.5 m between ponds, albeit at a rate of <0.5 mussel per trip. More recently, Banha *et al.* (2016)

recorded the adherence and continued attachment of *D. polymorpha* larvae to a mallard duck carcass during simulated swims ($\leq 0.5\,\mathrm{m\,s^{-1}}$). Equally, assuming an average flight speed of $75\,\mathrm{km\,h^{-1}}$, Banha *et al.* calculate that adhering larvae could be transported 145 km by ducks in a long-distance dispersal (LDD) event, with a 50% chance of survival.

The adherence (or biofouling) of *D. polymorpha* to other freshwater inhabitants such as Gastropoda, crayfish species, and dragonfly (Insecta: Odonata) nymphs has been well documented (*e.g.* Fincke and Tylczak, 2011). In particular, *D. polymorpha*, which is capable of secondary settlement and active reattachment, has been observed to attach, detach and subsequently reattach to Odonata nymphs and crayfish hosts when in search of a suitable substrate to inhabit (Fig. 2) (Ďuriš *et al.*, 2007; Hughes and Fincke, 2012). Interestingly, both Odonata nymphs and freshwater crayfish species are capable of short overland translocation between waterbodies. Moreover, these host species can shed their entire 'mussel load' upon cuticle moult, which is likely to deposit any adhering bivalves within the freshwater system (Ďuriš *et al.*, 2007; Hughes and Fincke, 2012). Surprisingly, our review of the literature indicates that the adherence of dreissenidae to mobile invertebrates has not been examined in the context of zoochorous dispersal.

Equally, no experimental studies concerning the role of birds – or indeed, large semi-aquatic and/or mud wallowing vertebrate species (*e.g.* otters, boars, muskrats etc.) – as possible vectors of ectozoochorous dispersal for *D. bugensis* or *C. fluminea* were obtained from the literature. Both Johnson and Carlton (1996) and Banha *et al.* (2016) have shown that waterbirds, such as ducks, can facilitate short-distance dispersal (SDD) of *D. polymorpha* veligers. However, over time, SDD may lead to LDD through multiple SDD events; collectively known as 'stepping-stone' dispersal (Fig. 1) (Coughlan *et al.*, 2017a, 2017b). Additionally, while Johnson and Carlton (1996) suggest that the rate of attachment of *D. polymorpha* to waterbirds is low, only scant experimental detail is provided. Studies such as Águas *et al.* (2014), Anastácio *et al.* (2014), and Banha *et al.* (2016) have highlighted the importance of aquatic invertebrate densities, water depth and exposure time upon the probability of aquatic invertebrate contact and attachment with waterbirds. Accordingly, the density of waterbirds will also influence the probability of contact with aquatic invertebrates and subsequent bird-mediated ectozoochorous dispersal (Coughlan *et al.*, 2017a). While ectozoochorous dispersal of *D. bugensis* and *C. fluminea* has not been examined, these species are likely to adhere to waterbirds in a similar fashion to *D. polymorpha*. In particular, the production of ctenidial mucillagineous (byssal) threads by juvenile *C. fluminea* are thought to aid floatation, zoochory and anthropogenic dispersal (McMahon, 1982).

If adherence is maintained, bivalves will need to survive the translocation process. This will likely become particularly arduous should a vector leave the aquatic medium. Ricciardi *et al.* (1995) indicated that adult *D. polymorpha* can survive (77.5% of specimens) 24 hrs aerial exposure at 30 °C and 50% relative humidity (RH). Greater survival (96.7%) was observed under colder conditions (20 °C and 50% RH). In contrast, only 40% of *D. bugensis* specimens survived 24 hr exposure to these colder conditions (20 °C and 50% RH). In addition, Byrne *et al.* (1988) observed a 50% mortality rate in adult *C. fluminea* aerially exposed to 25 °C and 53% RH for 73 hrs. However, specimens exposed to warmer conditions (35 °C and 53% RH) displayed 50% mortality after 24 hrs. Recently, Coughlan *et al.* (2015a, b) measured the microclimatic conditions found within the plumage of mallard ducks. While temperature and RH were found to vary with the external anatomical surfaces (*e.g.*, posterior neck, crural, crissum) of *A. platyrhynchos*, on average, ducks displayed temperatures of between 21 and 33 °C, and RH between 58.4 and 72.8%. Therefore, we surmise that even at the highest temperature and lowest RH combination found within mallard plumage, entangled adult *D. polymorpha* and *C. fluminea* may survive for up to 24 hrs, if not longer. Bivalves adhering to the feet of waterbirds are likely to be exposed to cooler temperatures, particularly in more temperate regions. However, temperature and humidity will depend on seasonal and local conditions.

3.3 Post dispersal

A suitable receiving environment is essential for successful dispersal (Coughlan *et al.*, 2017a). Freshwater fish do not leave the aquatic medium, and waterbirds often excrete faecal matter within aquatic sites. Thus, it seems reasonable to conclude that if bivalves survive endozoochory, they can be deposited within suitable freshwater habitats. Equally, detachment of an adhering organism can occur at any stage during ectozoochory when attachment fails. Waterbirds frequently move between freshwater sites, and therefore, it is likely that detachment can occur at a suitable location. In particular, bivalves adhering to birds *via* the 'grip' of their closed gape, may release when brought into contact with freshwater by a vectorbird. For example, Banha *et al.* (2014) observed that non-native snails (*Pysella acuta*) maintained attachment to a human vector (off-road vehicle) for *circa* 100 km, and subsequent detachment was promoted by contact with freshwater. Moreover, many waterbird species will often preen and wash themselves with freshwater, which may facilitate detachment of plumage enmeshed bivalves in a suitable environment.

4 Conclusion and recommendations

Our systematic search of the literature revealed only five studies that specifically attempted to examine zoochorous dispersal of invasive *D. polymorpha*, *D. bugensis*, or *C. fluminea*. Overall, when taken together, these publications suggest that zoochorous dispersal of invasive freshwater bivalves is possible. However, given that many potential vector species consistently move between invaded and non-invaded sites, and that the recorded rate of invasive spread is often low (*e.g.*, Caffrey *et al.*, 2016), zoochorous LDD may be a limited, if not rare, occurrence (Coughlan *et al.*, 2017a). Correspondingly, the recorded rate of natural up-stream dispersal and overland translocation of these invasive bivalves to adjacent (and hydrologically unconnected) waterbodies is slow (Voelz *et al.*, 1998; Kappes and Haase, 2012). Therefore, in agreement with postulations found within the literature, anthropogenic vectors likely present a higher potential for invasive bivalve dispersal (*e.g.*, Voelz *et al.*, 1998; Kappes and Haase, 2012; Marescaux *et al.*, 2012; Banha *et al.*, 2016; Solarz *et al.*, 2017).

Moreover, in agreement with Solarz *et al.* (2017), given the often limited resources available to tackle biological invasions, the challenging question of zoochorous dispersal cannot be a priority management issue. However, there remain substantial knowledge gaps concerning zoochorous dispersal of freshwater IAS, and in order to comply with good preventative biosecurity practices, potential vectors will need to be examined in more detail. Here, we identify key areas for further study, realistic opportunities for data collection, and management protocols for mitigation of IAS spread.

The ability of freshwater fish to disperse invasive bivalves merits further investigation. In particular, knowledge of gut retention times for a catalogue of potential vector species is needed (Gatlin *et al.*, 2013). Gut retention and survival of endozoochory can be analysed through *ex situ* feeding trials, focussing on the appearance of viable adult bivalves within gut or faecal samples. Such knowledge can be used to mitigate against further bivalve spread, by developing minimum quarantine times for fish caught and relocated for restocking purposes. Equally, other potential zoochorous vectors also need to be considered. For example, large semi-aquatic mammals have been shown to externally transport various aquatic invertebrates (Waterkeyn *et al.*, 2010). Moreover, possible dispersal of bivalves by other freshwater inhabitants such as crayfish, freshwater turtles, and Odonatanymphs should be examined in greater detail. While management of natural dispersal by vector organisms is problematic in the extreme (Solarz *et al.*, 2017), any animal which is deliberately taken from an invaded site, or equally, a site classified as being at risk of invasion, should be examined for the external adherence of 'hitch-hikers'. This is of particular importance if the animal is to be relocated and released into an uninvaded site.Awareness of zoochory and the importance of incidental *in situ* data collection needs to be promoted. A variety of nature enthusiasts, photographers, ecologists, conservationists, game hunters, wildlife and fisheries officers, bird ringers and field ornithologists come in contact with, deliberately observe, and often handle a variety of wildlife. It is not unlikely that instances of zoochory have been observed but remain undocumented. Notable examples include Green and Figuerola (2005) and Tøttrup *et al.* (2010), who documented the adherence of live cockle *Cerastoderma edule* to shorebirds ($n = 4$), and the attachment of non-native barnacles (up to >30 individual adult specimens) to migratory lesser black-backed gulls *Larus fuscus* ($n = 7$), respectively. Moreover, inseveral studies the combing of plumage has highlighted the adherence of invertebrates to waterbirds (*e.g.*, Reynolds and Cumming, 2015). Therefore, in order to accurately determine the frequency of bird-mediated ectozoochory, bird ringers and game hunters should be incentivised to work with research groups to provide greater access to samples. Citizen science initiatives to increase the collection and cataloguing of such observations across all potential vector taxa should be encouraged by IAS managers and research groups. Equally, as part of citizen science initiatives, anglers or game hunters should be encouraged to examine gut contents of caught fish or birds and report any intact adult bivalves found.

While this review has focused on zoochorous dispersal of invasive freshwater bivalves, a growing body of research suggests zoochory may contribute to the spread of a wide variety of IAS, including gastropoda, amphipoda and freshwater arthropoda (*e.g.*, juvenile crayfish) (Swanson, 1984; Reynolds *et al.*, 2015; Green, 2016). Notably, New Zealand mud snails (*Potamopyrgus antipodarum*), an emerging freshwater invader in the USA, has been shown to survive gut passage through several fish species (see Bruce *et al.*, 2009). Accordingly, the incorporation of zoochory biosecurity measures (*e.g.*, quarantine times) is urgently required within IAS management strategies to mitigate against local invader spread.

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Author contributions

NEC conceived and designed the review; NEC and ALS conducted the review and analysis; all authors contributed to the writing of the manuscript, which was led by NEC.

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