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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 — Zoochérie 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 (zoochérie) 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 envahissantes à d’autres organismes nous ont incité à évaluer l’importance de la zoochérie 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 intériorément des spécimens adultes viables de D. polymorpha et C. fluminea. En outre, la littérature indique que les veligers et les D. polymorpha juvéniles peuvent adhérer aux surfaces externes des oiseaux d’eau. Dans l’ensemble, la littérature suggère que la dispersion par zoochérie des bivalves envahis 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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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., 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; Douka 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 zoochoric 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 endozoochoric) 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., epizoan, entozoochory, 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
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; Tuckeret 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...
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 species (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 (≤0.5 m s⁻¹). Equally, assuming an average flight speed of 75 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) (Duris 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 (Duris et al., 2007; Hughes and Fincke, 2012). Surprisingly, our review of the literature indicates that the adherence of dreissenids 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 mucillaginous (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 Odonatanymphe 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, in-seeal 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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