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INVASION NOTE

Passive transport of a zebra mussel attached to a freshwater fish: A novel *Dreissena* dispersal mechanism?

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Abstract Darwin recognized the potential significance of animal-assisted dispersal for the geographic distribution of freshwater species. Phoretic interactions are assumed to contribute to the secondary (post-establishment) spread of invasive freshwater invertebrates, but vertebrate animals reported to disperse invasive bivalves are limited to amphibians and waterfowl. We present evidence of a novel phoretic interaction between the zebra mussel (*Dreissena polymorpha*) and a freshwater cyprinid minnow, the lake chub (*Couesius plumbeus*). To our knowledge, this is the first field-documented case of phoresis involving a freshwater bivalve and a fish. We suggest that this interaction will exacerbate risks of within-basin spread of zebra mussels via fish migration and overland transport of mussels by anglers carrying baitfish from invaded waterbodies.

Keywords Bivalve · Dispersal · *Dreissena* · Freshwater · Invasive species · Phoresy · Vector · Zoochory

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While humans play an overwhelmingly predominant role in introducing species to new biogeographic regions (Ricciardi 2007), both human and natural vectors can drive secondary (post-establishment) spread of species within any given region. Among the natural vectors often implicated in this process are animals that passively disperse life stages of less mobile animals and plants—an interaction variously known as phoresy, phoresis, or zoochory (Coughlan et al. 2017; Bartlow and Agosta 2021). The process is more likely to aid the dispersal of resistant dormant stages (e.g., eggs, seeds, cysts, spores, gemmules, statoblasts), but it can also contribute to the spread of active juvenile and adult organisms whose traits enable them to exploit the transport conditions. Diverse freshwater invertebrate taxa have been observed in phoretic interactions with vertebrate animals, which can have significant implications for range expansions (e.g., Reynolds et al. 2015; Green 2016). For example, Darwin (1878, 1882) suggested that some freshwater invertebrates are transported by waterfowl; he reported the case of a living juvenile unionid mussel (*Elliptio complanata*) attached to the foot of a blue-winged teal (*Spatula discors*) collected in the northeastern United States. Although there have been several anecdotal reports of freshwater bivalves clinging to the appendages of birds, amphibians and aquatic arthropods (e.g., Kew 1893; Coughlan et al. 2017; Bartlow and Agosta 2021), physical evidence demonstrating mechanisms of phoretic dispersal

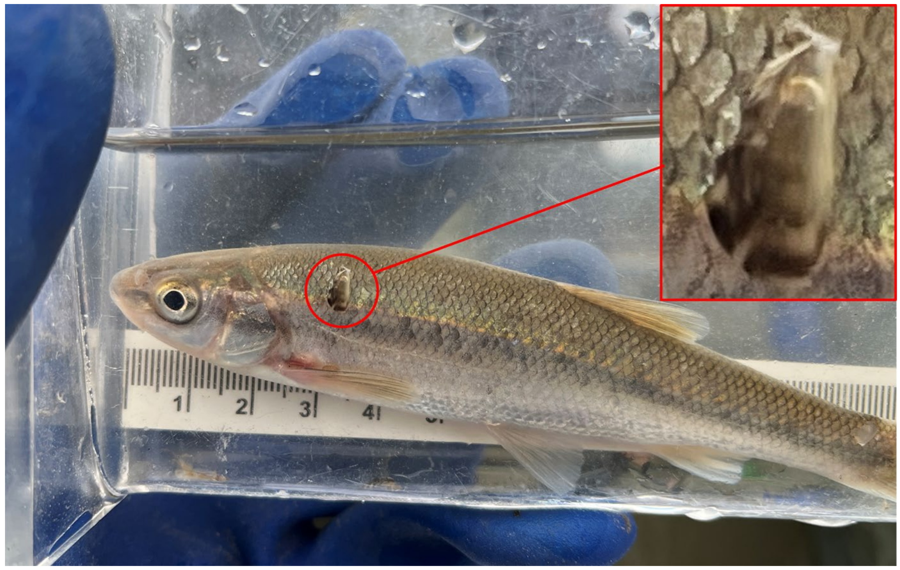

Fig. 1 Juvenile zebra mussel byssally attached to a cyprinid fish, lake chub (*Couesius plumbeus*). Photo by Jaclyn Hill

of freshwater bivalves is rare (but see Zelaya and Marinone 2012).

Here, we report a novel phoretic association between the zebra mussel (*Dreissena polymorpha*) and a freshwater fish. We found a living juvenile zebra mussel (5.9 mm length) byssally attached to the lateral scales of a 156 mm lake chub (*Couesius plumbeus*), a native cyprinid fish that was collected from Lake Témiscouata, southeastern Quebec, in a fyke net set for 23 h on October 20, 2022 (Fig. 1). Lake Témiscouata is the second largest lake south of the St. Lawrence River in Quebec, with a surface area of 67 km^2 and an average depth of 32 m. The lake is popular for fishing, boating and recreational use (OBVFSJ 2017) and is within the St. John River watershed shared by Quebec, Maine and New Brunswick. Lake chub is a benthic species typically found in shallow waters of lakes (Scott and Crossman 1973). The fish carrying the mussel was captured near a macrophyte bed in which juvenile zebra mussels were conspicuously attached to the stems of invasive Eurasian milfoil (*Myriophyllum spicatum*) and various native plant species. The zebra mussel, a highly invasive aquatic species in North America, was first reported in Lake Témiscouata by the Quebec government in September 2022 (MFFP 2022), but was likely established in the lake at least 2–3 years earlier.

To our knowledge, this is the first field observation of a phoretic association involving a non-larval freshwater bivalve and a fish. Whereas unionid mussels have evolved a commensal or ectoparasitic relationship with freshwater fishes in which mussel larvae (glochidia) attach to the gills and fins of specific fish hosts for dispersal, the life cycle of dreissenid mussels (*Dreissena* spp.) includes a free-living planktonic larval stage (the veliger) that lives in the water column for as long as a month prior to settlement and metamorphosis (Sprung 1989; Ackerman et al. 1994) and can thus be dispersed by waves and outflowing rivers. Further dispersal occurs by newly-settled and small juvenile mussels actively detaching from their substrates and floating away, using a thin mucous thread from either the foot or the siphon as a drag line to allow passive transport by water currents (Ackerman et al. 1994)—a process termed 'post-metamorphic drifting' (Martel 1993). We suggest that post-metamorphic drifting provides zebra mussels with opportunities to adventitiously attach to larger animals, such as those that frequent benthic or nearshore areas of lakes. Macrophytes are preferential settlement sites for veliger larvae (Lewandowski 1982; Bodamer and Ostrofsky 2010). After initial settlement on plant stems, juvenile mussels can detach their byssal threads and drift in the water column until they encounter other surfaces suitable for reattachment, which we believe led to the phoresis described here. Owing to their proximity to preferred zebra mussel settlement sites, benthic and phytophilous fishes are more likely to serve as transport vectors for juvenile mussels.

Reviews of the dispersal mechanisms of freshwater animals, including invasive species such as zebra mussels, do not mention this particular phoretic interaction (e.g., Carlton 1993; Bilton et al. 2001; Kappes and Haase 2012; Coughlan et al. 2017; Bartlow and Agosta 2021). No published cases were found by a literature search of Web of Science (November 6, 2022) using the following search string: *Dreissen* AND (zoochory OR phore* OR dispers* OR transport) AND fish*. Reports of a phoretic association of veligers and juvenile zebra mussels with vertebrates are limited to a single case study that experimentally manipulated small-scale ectozoochorous dispersal on living waterfowl (Johnson and Carlton 1996). Voskresensky (1966) reported a European freshwater clam (*Sphaerium corneum*) attached to the fin of a tropical freshwater fish (Gourami, *Trichopodus trichopterus*), but this interaction was likely observed in an aquarium (V. Radashevsky, Russian Academy of Sciences, personal communication). Similarly, there are few documented cases of juvenile and adult marine mytilid mussels dispersed by fishes; in each of these cases, the mussel was attached to a parasitic copepod anchored onto the fish (e.g., Mackenzie et al. 1974; Van Banning 1974). Nevertheless, we speculate that the occurrence of zebra mussel-fish phoresis is not as extremely rare as the lack of reporting suggests.

The significance of this phoretic association for dispersal remains to be determined, but we can hypothesize a few potential consequences for zebra mussel invasions. Fish could aid rapid diffusive spread of zebra mussels throughout a large heterogeneous waterbody, notably into connected waterways (e.g. canals, tributaries) and upstream areas accessible to fish but inaccessible to drifting mussel larvae and individuals attached to rafting material. Settled mussels are more commonly found attached to invertebrates possessing chitinous external structures, notably dragonfly nymphs, crayfishes, and amphipods (Fincke et al. 2009; Coughlan et al. 2017; Kenderov 2017). As these animals are not very mobile over long distances, and arthropods will shed any attached mussels during moulting, dispersal opportunities offered by such associations might be quite limited. By comparison, dispersal on fish would be less spatially and temporally restricted within hydrologically connected systems. Moreover, attachment of inconspicuous juvenile mussels to small cyprinid fishes used by anglers as baitfish could facilitate saltatory spread of the zebra mussel, e.g. through overland transport in bait buckets and subsequent dumping of live bait in other water bodies. Detailed inspections of fish collected from mussel-invaded lakes are needed to estimate the frequency of this phoretic association, as a first step toward estimating risk of dispersal.

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Data availability Not applicable.

Declarations

Conflict of interest The authors declare no conflict of interest.

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