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The status of the Duck Mussel, *Anodonta anatina* (Linnaeus, 1758), in Lough Derg, Shannon River, following the arrival of three invasive bivalves

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Abstract. The Zebra Mussel, *Dreissena polymorpha*, was introduced to Lough Derg, in the Shannon catchment, Ireland, during the early 1990s. Its presence led to the decline of the native Duck Mussel, *Anodonta anatina*, its empty shells remaining at lake depths to 11 m. *Dreissena polymorpha* shells were recovered throughout the lake to depths over 30 m. The Asian Clam, *Corbicula fluminea*, was first recorded in Lough Derg in 2011 and has also extended its range beyond 30 m, although it was not found in the most southern region of the lake. The Quagga Mussel, *Dreissena bugensis*, first found in 2021, has locally displaced *D. polymorpha*. Exposed shells of all these species provide a settlement surface for byssal attachment and a change to sediment habitats, with their shells likely to provide refuges for other invertebrates.

Key words. *Corbicula*, *Dreissena*, benthos, introduced, local extinction, invasive species

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Introduction

Unionids, such as *Anodonta anatina* (Linnaeus, 1758) (Unionidae), supply an ecosystem service of nutrient recycling by providing structure to a habitat (Vaughn *et al.* 2018). Since the early 1990s three invasive, suspension-feeding bivalves have colonized Lough Derg, Ireland, a large lake on the Shannon River, bordered by the counties of Clare, Galway, and Tipperary. In 1993/1994, the first invading bivalve to arrive was *Dreissena polymorpha* (Pallas, 1771) (Dreissenidae), which led to the decline of the native unionid, *A. anatina* (Minchin *et al.* 2002). Another invasive mussel, *Dreissena bugensis* (Andrusov, 1897), which was first recognized in Lough Derg in 2021 (Baars *et al.* 2022), is now locally replacing *D. polymorpha*. *Dreissena* species have pelagic larvae enabling rapid spread and use a byssus for settlement. Whereas *Corbicula fluminea* (Müller, 1774) (Cyrenidae), first found in Ireland in 2011, lacks a pelagic larval stage; it can gradually spread over the sediment using pedal movements, or by production of a byssal thread which can act as a dragline, enabling dispersal by water currents (Minchin & Boelens 2018).

Anodonta anatina has a wide European range extending eastwards to Siberia and south to Pakistan (Sohail *et al.* 2017). In Ireland it is distributed in the Shannon and Erne catchments (Byrne *et al.* 2009) and in Lough Neagh (Anderson 1992). In lowland lakes, *A. anatina* lives in mud to marl sediments and is less frequent elsewhere in Ireland (Lucey 1995; Biodiversity Ireland 2025). The related *Anodonta cygnea* (Linnaeus, 1758) has not been recorded from Lough Derg. Like many unionids, *A. anatina* buries in the sediment, with the posterior shell normally exposed enabling respiration and feeding. *Dreissena polymorpha* can attach in sufficient numbers to the exposed shell to result in suffocation, as happened to the Lough Derg population (Minchin *et al.* 2002). Similar declines of unionid populations, in the presence of mussels, are widely known (Strayer *et al.* 2011). Such has been the decline of *A. anatina*, which is Vulnerable on the IUCN Red List of species in Ireland (Byrne *et al.* 2009). Exposed empty unionid shells lying on the sediment can provide continued settlement surfaces for mussels.

Dreissena polymorpha originates from the Ponto-Caspian region and has gradually expanded its range westward in continental Europe (Matthews *et al.* 2014); it has also spread to North America (Karatayev *et al.* 2007). It was first recorded in the lower Shannon River by McCarthy *et al.* (1998) and most probably arrived in 1993–1994 on the fouled hulls of ferried leisure craft from the British Midlands (Pollux *et al.* 2003). It rapidly spread through the Shannon Navigation by upriver transport on the hulls of craft and has become the most dominant bivalve in the Shannon. Elsewhere it spread by overland transmission with boats on trailers to lakes in separate river catchments (Minchin *et al.* 2002). *Dreissena polmorpha* can attain sufficiently high densities to act as a powerful ecosystem engineer (Karatayev *et al.* 2002; Zaiko *et al.* 2009; DeVanna *et al.* 2011) by removing energy from the water column by filtration and by depositing wastes into the benthos (Karatayev *et al.* 2007). In Ireland *D. polymorpha* has had a greater abundance in alkaline lakes than in rivers (Zaiko *et al.* 2014).

Corbicula fluminea was first found in Lough Derg in January 2011 (Minchin 2014), but by this time it had already become established in the Upper Shannon (Hayden & Caffrey 2013). It previously had been found in the freshwater tidal estuary of the Barrow River, south-east Ireland (Sweeney 2009). The genus *Corbicula* is native to Southeast Asia, the Middle East, Africa, and Oceania, and over several decades it has extensively colonized the Americas, elsewhere in Europe (McMahon 1982; Araujo *et al.* 1993), and recently New Zealand (Sommerville *et al.* 2025). The *Corbicula* form in Ireland has a shell morphology similar to *Corbicula leana* Prime, 1864 (Morhun *et al.* 2022) and has androgenic reproduction (Sheehan *et al.* 2019). There are three principle morphotypes in Western Europe (Pineur *et al.* 2011), and the "A/R" form would appear to be the invasive form in Ireland, consisting of an American ("A") form combined with the European ("R") form. The classification of the genus *Corbicula* now assigns form names to populations (Pigneur *et al.* 2014); these have been referred to in the past as *C. fluminea* in a broad sense (Lucy *et al.* 2012). Here the A/R form is referred to as *Corbicula* sp. On account of its high-filtration ability, it can reduce phytoplankton abundance (Pigneur *et al.* 2014), but it also has the capability of feeding on deposited organic matter in sediments (Majdi *et al.* 2014).

Dreissena bugensis is also capable of altering ecosystem function and is causing significant economic impacts (Strayer 2009; Higgins & Vander Zanden 2010). Like *D. polymorpha*, *D. bugensis* has spread westwards in Europe (Bij de Vaate *et al.* 2013) and to North America where its occurrence is extensive (Brown & Stepien 2010). It was first recorded in Lough Derg in 2021 (Baars *et al.* 2022) and likely spread downstream from Lough Ree, where it was probably introduced (Flynn *et al.* 2023).

This study describes the distribution of empty shells of *A. anatina* and living *D. polymorpha* and *Corbicula* and their shells at different depth zones in Lough Derg. It also describes a local expansion of *D. bugensis* in the lough.

METHODS

Study Area

Lough Derg is the largest lake on the Shannon River (Fig. 1) and has a surface area of 118 km^2, a mean depth of 7.5 m, and a maximum depth to 36 m (Bowman 1998). The main axis of the southern half of the lough has narrow troughs with depths >30 m (Bowman 1998). Water transparency in the lake is reduced by humic acids arising from peat water draining from midland bogs. The acidic water is subsequently buffered in the lough by carboniferous limestones to produce alkaline water with a range of pH 7.7–8.2 (Moriarty 1986).

Lough Derg water levels are controlled within a range of 156 cm, as the lake and the downriver reservoir provides a water supply for a power station (Jacobs Tobin 2024). Normally lake levels have a range of 50 cm.

Sampling Methods

A basket dredge was used to sample bivalves and their shells in sediments throughout Lough Derg at depths of 2–36 m. The dredge was towed at approximately 2 knots, cutting a groove in the sediments, and could collect shells over silt to gravel and stones without the dredge becoming buried. Retrieved samples were flushed with lake water over a 2 mm sieve. Both single and paired valves of *A. anatina* and both live animals and empty shells of the invasive bivalves were recorded as present or absent for each haul.

In 2021, selective sampling was done using the dredge in the southern region of the lake at depths of >30 m, and further sampling was made to the south of the 2021 front in 2024. The shallow bays of Dromineer, in 2018 and 2023, and Meelick, from 2022 to 2023, were further sampled with the dredge and by wading using a rake. Luska and Youghal bays were examined using a rake in 2023.

The charophyte *Nitellopsis obtusa* (N.A. Desvaux) J. Groves, to which mussels attached, was collected by using a grapnel at the same southern region of Lough Derg (Fig. 1) during 2017 and 2024.

A scraper, with a meshed pocket net, mounted on a 4 m pole was used to remove dreissenid mussels from pillars of a floating boardwalk 1 km down-river of Lough Derg during the summer or autumn of 2016, 2017, 2021, 2023, and 2025. During 2002 and 2024 the occurrence of dreissenid

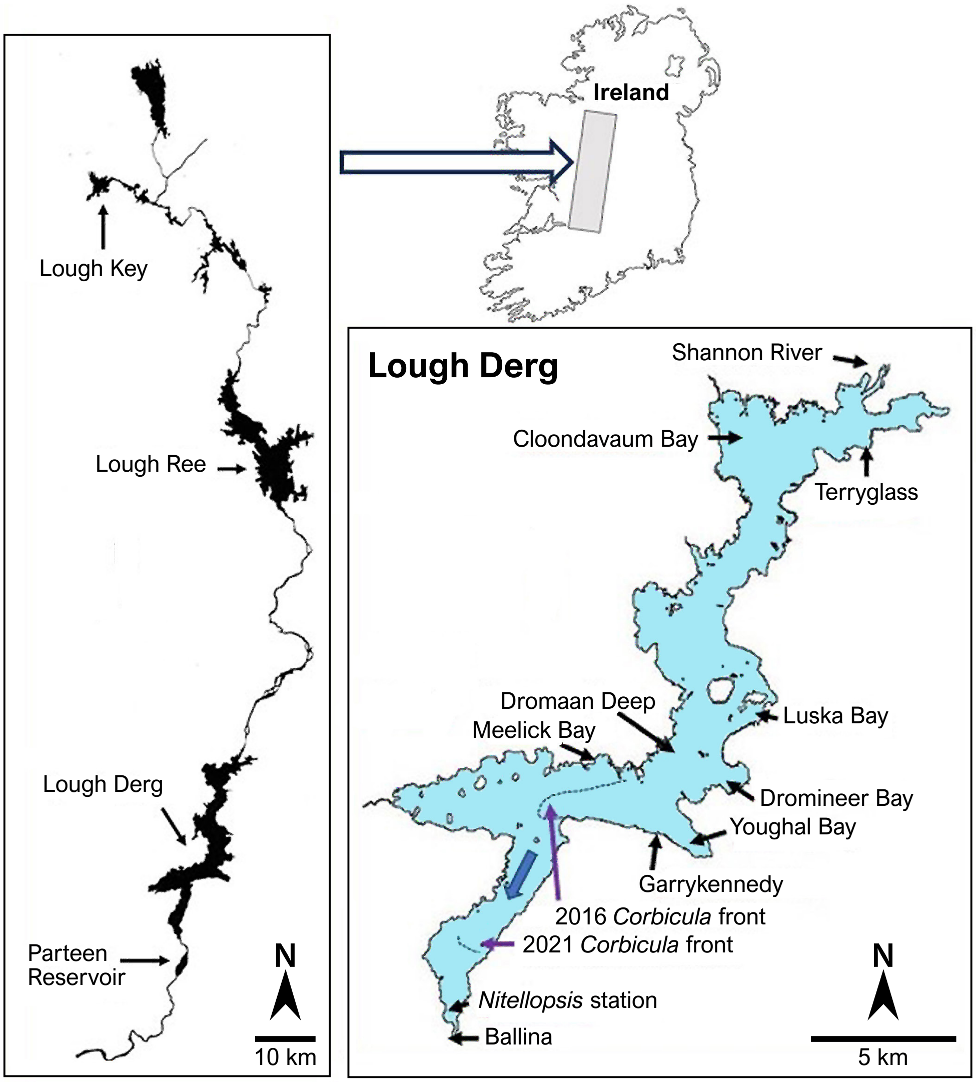

Figure 1. Lough Derg showing localities referred to in the text and position of *Corbicula* southward progressive fronts in 2016 and 2021.

bivalves was based on dredge samples taken nearby from gravel. From these samples, the relative proportions of *D. polymorpha* and *D. bugensis* were obtained.

Depths were measured using a Navman Fish 4500 dual-frequency sonar fishfinder at 200 kHz permanently mounted on a vessel hull. Presence of invasive bivalves was recorded either as living animals and/or empty shells at seven depth classes of 5 m intervals. The presence of *A. anatina* animals and shells was recorded at each meter of depth.

Results

Dredge sampling effectively collected shells of *Anodonta anatina* and animals and shells of *Dreissena polymorpha* and *Corbicula* based on a total of 1033 dredge hauls made from 2011 to 2016 at 708 different sites over a wide area of the lake. Dredge sampling since 2021 will also have involved the presence of living *D. bugensis* and their empty shells at depths of 2–36 m. Empty shells of *A. anatina* occurred at depths of 2–11 m, a depth range representing more than half the lake's area. During the dredge study of 2011–2016, only two live specimens of *A. anatina* were dredged, and none were taken by dredging since then. These living specimens, collected in 2015, one of 53 mm shell length at 4 m and one of 36 mm at 10 m. Both individuals were extensively fouled with *D. polymorpha*. Empty shells of *A. anatina* were recovered from mud (68%) and silt (17%) (Fig. 2), and most were heavily fouled with *D. polymorpha* (Fig. 3); shells were most frequent at depths of 3–5 m and seldom were recovered from depths >9 m (Fig. 4). These shells were

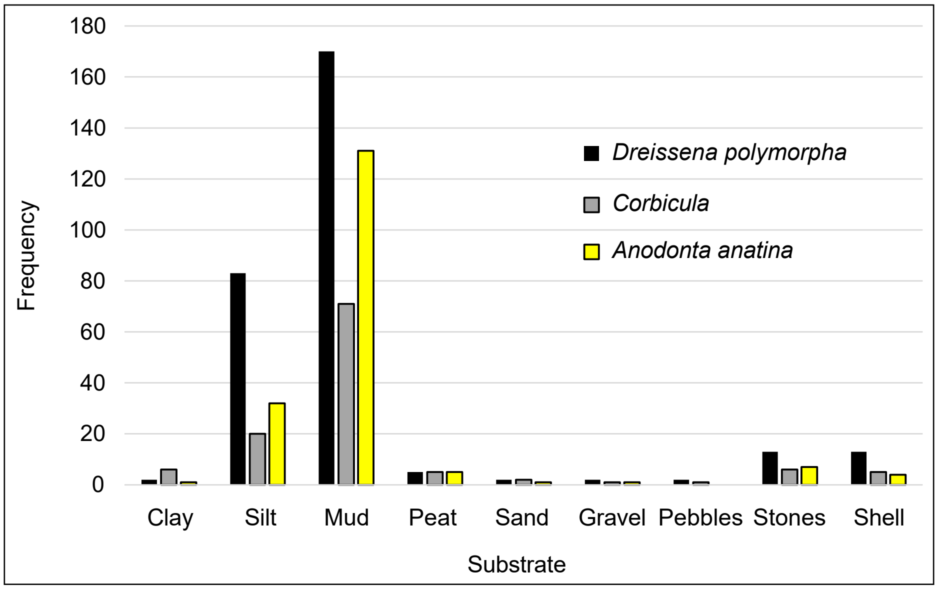

Figure 2. Substrates where bivalves were recorded 2011–2016.

Figure 3. A, *Dreissena polymorpha* attached to an *Anodonta anatina* shell (February 2003). **B**, heavy settlement of *D. polymorpha* (June 1998). **C**, *Corbicula* with attached *D. polymorpha* and muddy tube (arrowed) of the amphipod *Chelicorophium curvispinum* (June 2014).**D**, recently settled *D. bugensis*, with single individual of the large, pale form, attached to the charophyte *Nitellopsis obtusa* (July 2021).

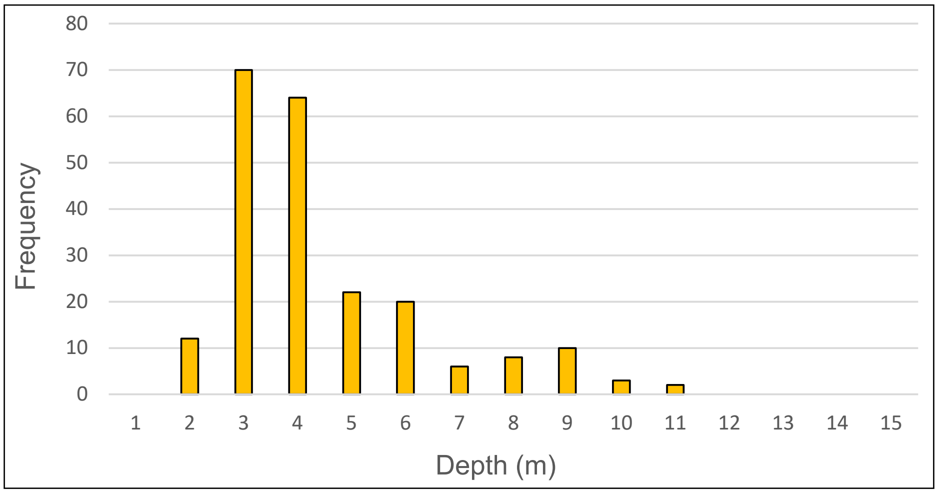

Figure 4. The frequency with depth of mainly paired *Anodonta anatina* shells at depths of 1 m intervals.

predominantly paired valves showing little corrosion. *Anodonta* shells were locally abundant in bays and in areas with current-washed gravels and stones, but less frequent where there were rooted aquatic plants.

Dreissena polymorpha had become abundant by 2002, occurring throughout the shallow regions of Lough Derg and extensively settling on shell of its own species, empty *A. anatina* shells, and on other natural as well as anthropogenic surfaces. Since 2011, deeper-water dredging found live *D. polymorpha* and shells overlying muddy sediments down to >30 m (Fig. 5). While these samples were few, empty shells and living individuals of *D. polymorpha* were confirmed at these greater depths. Apart from attaching to its own empty shells, *D. polymorpha* was rarely found adhered to sphaeriid bivalves, gastropods, aquatic plants, and autumn leaves at depths exceeding 25 m.

Small *D. polymorpha* attached to aquatic mosses in shallow water, and during 2017 it was abundant on *Nitellopsis obtusa* at depths of 3–5 m in the southern part of the lake where there was a noticeable water current (Fig. 1). In 2024, no *D. polymorpha* were found attached to this charophyte, whereas *D. bugensis* was present in abundance (Fig. 3).

Corbicula occurred in the northern and mid-section of the lake to depths of >30 m by 2016 (Fig 5). Despite the small number of samples in the deepest parts of the lake, small living individuals were found at these depths as part of the progressive southward frontal expansion. By 2016 the most southern extent of the population formed a front above the lower section of the lake (Fig. 1). Five years later, this front had extended south by 6.5 km and to depths of 32 m. Sampling in 2024 indicated no known further southward progression to the south of this 2021 front.

In shallow bays, *Corbicula* had expanded into the shallows of Dromineer Bay by 2018 when it was found at a depth of 3 m. By the summer of 2023, it had further encroached into this bay and was found in water as shallow as 0.30 m. In 2022, it was found in the shallow marl sediments of Meelick Bay, with no specimens found deeper than 2 m. In 2023, specimens were present at a depth of 0.30 m. *Corbicula* was not found in the shallows of Luska and Youghal bays (Fig. 1).

Dreissena bugensis was not recorded from scrape samples during 2016 and 2017. Following its presence in samples taken during 2021, which included a pale shell morph, *D. bugensis* increased in abundance (Fig. 3). It had become the dominant species by 2022, and *D. polymorpha* had almost been replaced by 2025 (Fig. 6).

Discussion

The distribution of one native and two invasive bivalves were examined in Lough Derg, the largest lake on the Shannon. Live *Anodonta anatina* were originally common in shallow bays, and there were reports of swimmers' feet being cut by their presence (M. Gill pers. com. 1997). From 2000 to 2002, empty *Anodonta* and *D. polymorpha* shells accumulated in windrows along shores (Minchin *et al.* 2022). The *A. anatina* population is thought to have declined at this time due to mussel fouling. Such declines of unionids due to mussel fouling were already known elsewhere (Strayer & Smith 1996). Widespread dredging in Lough Derg found empty *A. anatina* shells at depths of 2–11 m, but most frequently at 3–5 m. This distribution of empty shells most probably represents the original distribution of *A. anatina* before the arrival of *D. polymorpha*. However, empty shells of *A. anatina*

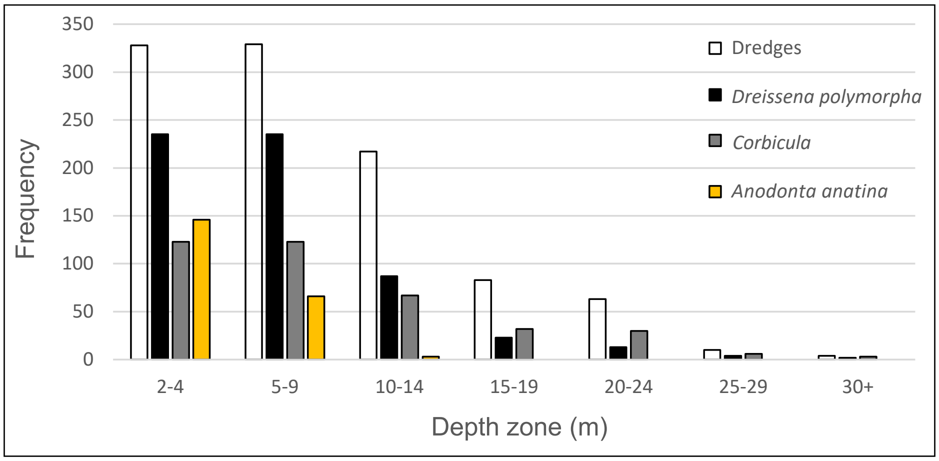

Figure 5. Dredge samples from 5 m depth zones for the presence of three bivalve species, 2011–2016. Open bars represent the number of dredge hauls.

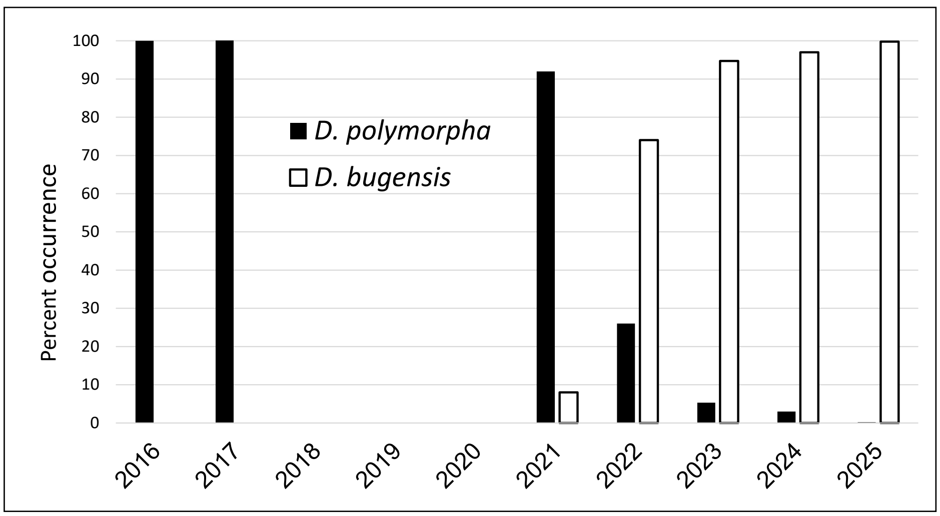

Figure 6. Decline of *Dreissena polymorpha* (black) 1 km south of Lough Derg and replacement by the *D. bugensis* (open bars), 2017–2025. There was no sampling at this site from 2018 to 2020.

in wadable depths were likely to have been either cast ashore (Minchin *et al*. 2022) or displaced by wave action beyond wading depth. The empty shells of long-dead *A. anatina* continued to provide a settlement surface for *D. polymorpha*. Below 11 m there were limited deposits of native shells from sphaeriid bivalves and small gastropods that could provide a surface for dreissenid mussel settlement. Since the 1990s, the greatest amount of shell material produced throughout the lake has been from *D. polymorpha*.

The arrival of *D. polymorpha* in Lough Derg was most probably in the southern region of the lake on the fouled hulls of watercraft from the Midlands of Britain (Pollux *et al*. 2003). This dreissenid had already become abundant in the reservoir below Lough Derg when it was first recognized in 1997 (McCarthy *et al.* 1998). It rapidly expanded in Lough Derg to produce a peak of abundance in 1999–2001 (Minchin *et al*. 2002). Such was its abundance that scrape sampling at lake quays included >5,000 individuals/m^2 and had a wet biomass of 2.5–3.0 kg/m^2 (Minchin *et al.* 2005). During this period, *D. polymorpha* was seen attached to the posterior shell ends of living *A. anatina*, thereby obstructing siphonal function. Many *Anodonta* that were alive were lying on their side on the sediment surface. Soon after, their empty shells fouled with *D. polymorpha* were commonly seen scattered over the sediment at 1–3 m depths. During this outbreak period, *D. polymorpha* had also settled on aquatic plants in Lough Derg, as happened elsewhere on the Shannon River (Sullivan *et al.* 2010).

Deeper-water monitoring, mainly on fine sediments, did not take place until 2011. This followed the first record of *Corbicula* from the mid-lake muddy bottom at 25 m (Minchin 2014). From this initial region of the lake, *Corbicula* gradually expanded southwards at a rate of approximately 2.5 km/yr, to form the 2016 front (Minchin & Boelens 2018). By 2021, a new front had formed 6.5 km to the south along a trench of deep water; this later expansion had a slower progression, estimated at 1.3 km/yr. There has been no known continued southward progression since 2021. Individuals obtained from the deep-water trench region are generally small. At depths >20 m, few shells of *Corbicula* are longer than 20 mm. This might have been due to the fine sediments being unable to carry the weight of the thick shell. In the coarser sediments in two shallow bays, larger individuals were frequent. By 2018, *Corbicula* had become common further inshore in water as shallow as 3 m in Dromineer Bay, and later, by 2023, in water only 0.30 m deep. The appearance of *Corbicula* in Meelick Bay (Fig. 1) appears to be confined to depths of 0.30–2 m with a sediment containing marl (Minchin & Higgins 2023). *Corbicula* may be expected to arrive to other shallow bays in the future.

Since the arrival of *D. polymorpha* in Lough Derg in the 1990s, there was a second dreissenid mussel invasion almost 30 years later. *Dreissena bugensis* was first collected in 2021 in the Shannon River near Ballina, approximately 1 km below Lough Derg (Fig. 1). In the same year it was found within Lough Derg and Lough Ree (Baars *et al.* 2022). Estimated growth of *D. bugensis*, based on polymodal frequencies, indicated that it probably arrived in Lough Ree, upstream of Lough Derg in the Shannon about 2016–2017 (Flynn *et al.* 2023). Its arrival to Lough Derg was either via downriver dispersal of its pelagic larvae or more likely on hull-fouled watercraft. Lough Derg, being a polymictic lake, would ensure a rapid dispersal of larvae by wind forcing following a spawning event. Once established, *D. bugensis* became dominant in the southern region of the lake. Here in 2016 and 2017, *D. polymorpha* was the only species recorded. However, *D. bugensis* had all but replaced *D. polymorpha* by 2024–2025. Such dominance of *D. bugensis* has been reported elsewhere in Europe and North America (D'Hont *et al.* 2018; Strayer *et al.* 2019), and this dreissenid is expected to expand its range into the future.

The charophyte *Nitellopsis obtusa* was first found in 2016 and is established in the shallows of the southern end of Lough Derg and in the Parteen Reservoir. It lives at depths of 5 m, beyond the depth range of aquatic angiosperms (Minchin *et al.* 2017). In 2017, in southern Lough Derg with water currents, many *D. polymorpha* were found attached to the fine filaments of *N. obtusa* (Minchin *et al.* 2021). Within six years, this charophyte became fouled with only *D. bugensis*. Such settlement patterns are known elsewhere on the Shannon River in Lough Ree (Corcoran *et al.* 2023). In Lough Derg, dredged sediments of mud and gravel at the base of these plants contained quantities of small shells from both dreissenid species. This charophyte currently forms extensive meadows in both loughs Derg and Ree (Flynn *et al.* 2024), and its presence there is likely to capture settling dreissenid larvae, leading to a further contribution to shell production.

In areas with water currents and where there are firm natural and anthropogenic surfaces, with low sedimentation rates, continued settlements by dreissenids may be expected. Such areas had initially been colonized by *D. polymorpha*, which more recently was replaced by *D. bugensis*, which is adapted for colonizing deep-water lakes (Karatayev *et al.* 2021). *Corbicula*, with its preference for sediments, now provides additional surfaces on muddy and silty bottoms for the settlement of *D. bugensis*.

The subsurface drift of plant materials, including dead leaves, with attached *D. polymorpha* (Minchin *et al.* 2021) may have been of important in the initial colonization of deep water by this dreissenid. Shell of these first colonizers would have subsequently provided sites for the settlement of larvae and account for the formation of small clusters of dreissenid mussels which were obtained in the dredge samples. *Corbicula* shells have added to the availability of surfaces for the settlement of larvae. In the future, *D. bugensis* is likely to become an important contributor of shell material at depth. Dreissenid settlement may, in part, can be locally suppressed by *Chelicorophium curvispinum* (G.O. Sars, 1895), a Ponto-Caspian amphipod. This species produces muddy tubes attached to hard surfaces, including living bivalves (Fig. 3), and competing with dreissenids for settlement space.

There are other Ponto-Caspian species that are persistently spreading westward in Europe through connected waterways (De Vaate *et al.* 2002; Lipinskaya *et al.* 2020). Among these are benthic crustaceans, some already in Britain, and others poised to arrive (Copilas-Ciocianu *et al.* 2023). This change in habitat resulting from the large amount of shell present over a wide depth range in Lough Derg provides opportunities for non-native benthic crustaceans, as reported elsewhere (Bially *et al.* 2000; Zaiko *et al.* 2009; Burlakova *et al.* 2012).

CONCLUSION

Anodonta anatina is unlikely to recolonise Lough Derg in the near future. Iits empty valves continue to provide surfaces for the settlement of dreissenid mussels. The addition of dreissenid and *Corbicula* shells continue to accumulate over soft sediments occurring over a wide depth range. Such exposed shell material potentially provides habitat for non-native benthic crustaceans, in particular those from the Ponto-Caspian region. These crustacean species, already present in the Netherlands, pose a risk to Britain and subsequently to Ireland. The increase in shell deposits produced following the introduction of *Dreissena* and *Corbicula*, and the continued presence of *A. anatina* shell, may alter the future benthic composition in the lake. *Dreissena bugensis*, which is adapted for deep-water lakes, is likely to become abundant throughout Lough Derg.. However, should both *Dreissena species* decline in abundance, recolonization of Lough Derg by *A. anatina* from existing populations in rivers, may be possible.

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