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Research Article

Early stage of invasion of the quagga mussel (*Dreissena rostriformis bugensis*) within the interconnected lakes Lough Ree and Lough Derg of the Shannon River system, Ireland

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Abstract

Quagga and zebra mussels of the genus *Dreissena* are two of the most impactful freshwater invasive alien species that have spread widely across the globe. These species attach to natural and artificial substrates, form dense populations and filter large volumes of water causing ecological and economic damage. Following the quagga mussel's discovery in the Shannon River system in Ireland, this study assesses its local distribution, population density, relative abundance, and population structure in the interconnected lakes Lough Ree and Lough Derg in order to determine the likely year and location of its introduction. Polymodal length-frequency analysis was used to distinguish between year cohorts and estimate growth rates. The quagga mussel is established widely across both lakes and is settling on a range of artificial surfaces, natural substrates, dead shells, plant material, and other invasive bivalves. High densities of quagga mussels exceeding 20 000 individuals per m^2 were present on artificial surfaces in Lough Ree with total dreissenid densities reaching 26 758 per m^2. The relative abundance of quagga mussels to zebra mussels on natural substrates is high in Lough Ree (up to 94.7%) and low in Lough Derg (up to 16.8%). Two to four year cohorts were present at all sites, with quagga mussels attaining large shell sizes over 34 mm in length. Growth varied between sites with a maximum estimated yearly growth rate of 16.8 mm. The time and place of the quagga mussel's initial introduction in Ireland is still uncertain, but its widespread distribution, population structure, and high population density and relative abundance suggest it was first introduced to Lough Ree in 2016 or 2017.

Key words: bivalve, cohorts, distribution, dreissenid, length-frequency, population structure

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Introduction

Freshwater mussels of the genus *Dreissena* have proven to be successful and impactful invaders (Ward and Ricciardi 2007; Fahnenstiel et al. 2010; Higgins and Vander Zanden 2010). Originating from the Ponto-Caspian region (Son 2007), they have spread widely across Europe and North America (Bij de Vaate and Beisel 2011; Heiler et al. 2013; Karatayev et al. 2015) and continue to expand their range (Marescaux et al. 2012; Vanassche et al. 2014; Wakida-Kusunoki et al. 2015; Woźniczka et al. 2016; Catita et al. 2020; Babushkin et al. 2022). Ecological impacts arise as dreissenid mussels attain high biomass within invaded systems and filter large volumes of water (Higgins and Vander Zanden 2010; Strayer et al. 2019). High densities can lead to an alteration of phytoplankton biomass and composition (Higgins and Vander Zanden 2010), increased water clarity (Higgins and Vander Zanden 2010), modified benthic habitat structure (Ward and Ricciardi 2007; Mayer et al. 2014), the benthification of resources (Higgins and Vander Zanden 2010; Mayer et al. 2014), and declines in native filter feeding taxa (Ward and Ricciardi 2007) while facilitating increases in macrophytes (Crane et al. 2020) and some benthic invertebrates (Ward and Ricciardi 2007). Economic impacts arise due to their ability to attach to hard structures leading to the fouling of boat hulls and reductions in flow in abstraction pipework (Connelly et al. 2007).

In Europe and North America the arrival of the zebra mussel *Dreissena polymorpha* (Pallas, 1771) has been followed by that of the quagga mussel *Dreissena rostriformis bugensis* (Andrusov, 1897) (Mills et al. 1993; Molloy et al. 2007; Grigorovich et al. 2008; Woźniczka et al. 2016). While these congeners coexist in some locations (Zhulidov et al. 2010), quagga mussels often displace zebra mussels within their invasive range (Hetherington et al. 2019; Strayer et al. 2019). Quagga mussels are hypothesised to outcompete zebra mussels in their occupied habitat due to greater energetic efficiency which facilitates activity at much lower temperatures and survival on lower concentrations of food (Baldwin et al. 2002; Stoeckmann 2003; Zaiko et al. 2014; Karatayev et al. 2015), conditions which are often present in zebra mussel invaded systems due to over-filtration (Karatayev et al. 2015). A higher tolerance to low oxygen concentrations may also enable the quagga mussel to inhabit oxygen-poor water that the zebra mussel is unable to occupy (Karatayev et al. 2011). Further, quagga mussels can attain greater lengths and weights than zebra mussels (Stoeckmann 2003) and at low food levels the quagga mussel can outgrow the zebra mussel (Baldwin et al. 2002). Higher growth rates and a larger range of growth rates within systems suggest the quagga mussel is more flexible in fluctuating environments (Metz et al. 2018).

The zebra mussel was unintentionally introduced to Ireland to lower Lough Derg (LD) in 1993/1994, most probably on the hulls of imported leisure craft from the midlands of Britain (Pollux et al. 2003). By 2000 it had spread throughout the Shannon River system and to interconnected lakes (Minchin et al. 2002). Three years following the introduction of the zebra mussel to LD and Lough Ree (LR) (1994 and 1996 respectively), intense settlements occurred which resulted in separate and distinct outbreak periods of exceptionally high settlement and population densities in each lake, after which populations declined to more sustainable densities (Zaiko et al. 2014). In June 2021 *D. r. bugensis* was discovered incidentally for the first time in Ireland in lower LD at Killaloe (Baars et al. 2022). A rapid assessment in July and August of 2021 showed that it was widely distributed within the interconnected lakes of LR and LD (Baars et al. 2022). Highest densities of 4000 to 5000 individuals per m^2 were present on artificial surfaces in southern LR (Baars et al. 2022). Quagga mussels accounted for over 70% of the dreissenid community at Glasson in LR and sampled mussels attained a maximum size of 34 mm (Baars et al. 2022).

Polymodal length-frequency distributions have enabled the separation of year cohorts of dreissenids in several studies (Bij de Vaate 1991; Griffiths et al. 1991; Mills et al. 1993; Nalepa et al. 1995; McMahon 2011; Wong et al. 2012; Aldridge et al. 2014; Balogh et al. 2018). Growth and survival may also be inferred from length-frequency distributions when there is little overlap between the year cohorts during the early stages of invasion (Nalepa et al. 1995). Following the discovery of the quagga mussel in LR in June 2021, we questioned when and where it first became established and how widely it has spread across lake substrates. This study assesses the distribution of the quagga mussel across LR and LD, the relative abundance of quagga mussels compared to zebra mussels on natural substrates and artificial surfaces, and the population structure of the quagga mussel at a range of shallow sites (under 6 m) in order to determine the likely time and location of its introduction and provide an indication of growth rates.

Materials and methods

Lough Ree (LR) and the downstream Lough Derg (LD) are interconnected lakes within the agricultural River Shannon catchment, separated by approximately 60 km of river channel. Lough Ree has a surface area of 105 km^2, a maximum depth of 34 m, and a mean depth of 6.2 m. Lough Derg has a surface area of 118 km^2, a maximum depth of 36 m, and a mean depth of 7.5 m. Both lakes have high hardness levels and alkaline pH due to their mainly limestone catchment basin and are considered to have high nutrient levels. Both lakes have supported extremely high levels of zebra mussel in the past (Zaiko et al. 2014) and are expected to be equally suitable for the quagga mussel.

A basket dredge (described in Minchin and Boelens 2018) was used to sample natural substrates in both LR and LD to a depth of 32.5 m, with one dredge per location. The dredge is towed to sample the lake substrate and the 5 mm mesh allows the fine sediments to be filtered during sampling. Typically mussels on soft sediments attach to conspecifics or debris but smaller individuals may be disproportionally lost during sampling. It is possible that this leads to a conservative estimate of the smaller cohorts, although grab sampling conducted by the authors indicate that there is limited loss of this size cohort during dredge sampling.

Sites were chosen on the basis of obtaining a good spatial distribution with locations ~ 50 to 300 m apart. Locations of substantial depth were also sought out in order to record a maximum depth for the quagga mussel. Presence or absence of the quagga mussel on natural substrates was recorded for 212 locations during July and September 2021 and April 2022 and is presented alongside 8 scrapes on artificial surfaces in Fig. 1 with further details in the Suppl. material 1. Dredge samples taken during July and September 2021 were used to calculate the relative abundance and relative biomass of dreissenid mussels at 11 sites (R1–R6 in LR and D1–D5 in LD) (Suppl. material 2).

A scraper, on the end of an extendable pole, with either a 10 or 15 cm width blade was used to detach mussels from 1.5 to 1.8 m depth on artificial surfaces (pontoons or quay walls) in LR. Three sites (Portrunny Harbour, Hodson Bay, and Killinure Point) were sampled initially during July 2021 and were revisited in either December 2021 or January 2022. Mussels were collected within a net pocket with a mesh size of 500 μm in order to capture the smaller individuals dislodged from the hard surface during scraping. Scrapes were spatially distributed to represent the site and estimated densities were calculated depending on the length (30 cm) and number of scrapes (between 3 and 6).

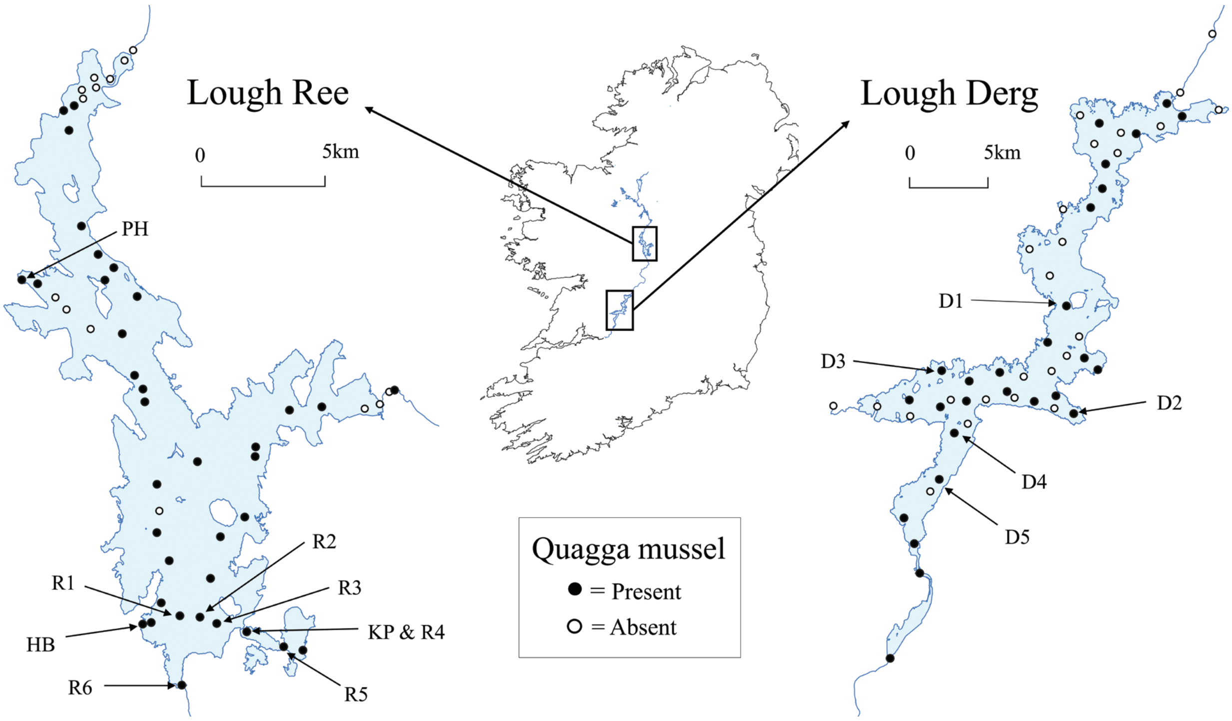

Figure 1. The Shannon River system with Lough Ree and Lough Derg enlarged with circles showing quagga mussel presence (black) and absence (white) recorded in 2021 and 2022. A total of 212 dredges on natural substrates and 8 scrapes on artificial surfaces are shown. Scrapes on artificial surfaces are notated for sites Portrunny Harbour (PH), Hodson Bay (HB) and Killinure Point (KP). Dredges on natural substrates are notated for sites R1–R6 and D1–D5. Some dredge presence and absence locations were removed from both LR (n = 6) and LD (n = 111) in order to provide clarity in the map at this scale. See details in the Suppl. material 1.

Species identifications and processing were completed in a laboratory. Morphological differences, primarily the angle of the transition between the ventral and dorsal surfaces (Teubner et al. 2016), were utilised to distinguish between dreissenid species. Small individuals required microscope examination at × 40. Total weights by species were recorded per sample using a balance accurate to 0.1 g.

Mussel shell length was measured using a callipers down to the nearest mm. In LR, population profiles were produced from scrape samples taken at Portrunny Harbour, Hodson Bay and Killinure Point. In LD, dredge samples were used to produce population profiles for four sites from depths 5–6 m at D1, D2, D3 and D4. Quagga mussel populations on artificial surfaces in LD were previously found to be low (Baars et al. 2022) and were therefore omitted from this study as they would not have provided population profiles of sufficient resolution for analysis. Individuals from sites R1–R6 were not measured at the time due to time constraints and therefore could not be used to produce population profiles.

In order to detect the presence of yearly cohorts, a polymodal length-frequency distribution analysis was conducted within RStudio version 1.4.1103 (RStudio Team 2021) using the package Mixdist version 0.5-5 (Macdonald and Du 2018) with some enhanced and additional features provided by Macdonald. Mixture analyses of all measurement sites were conducted using the general procedure outlined in Macdonald and Pitcher (1979) and provide a graphical basis for separating mixed distributions into their parts, interpreting each mode as an individual cohort and providing summary statistics and X^2 goodness of fit. Estimations of yearly growth rate were deduced for each site by calculating the difference in modelled mean shell lengths between two successive cohorts within the same sampling period.

Results

Lough Ree

Quagga mussels were widespread on natural substrates occurring at 35 of 53 locations in LR and are now established lake-wide, except at the most northern section of the lake near Lanesborough (Fig. 1), and are present at depths from less than 1 m to 31 m. The relative abundance of quagga mussels to zebra mussels on natural substrates in LR ranged from 7.1 to 94.7% (Table 1). Relative biomass was comparable and ranged from 16.2 to 92.3% (Table 1). The relative abundance of the quagga mussel on hard surfaces was more consistently higher and ranged from 61.1 to 67.6% in July 2021 with this range increasing to 66.1 to 85.5% in December 2021 and January 2022 (Table 2). Densities of 20 223 quagga mussels per m^2 were recorded on artificial surfaces at Killinure Point in January 2022 which was over four times the density recorded at the same site in July 2021 by Baars et al. (2022) (Table 2). This increase in density is largely due to the presence of the young-of-the year (group '0') (Fig. 2).

Shell lengths of 5868 quagga mussels less than 1 to 34 mm were measured from the three scrape sites within LR. Length-frequency distributions produced from the July samples revealed three modes, each presumed to represent a separate year cohort – groups '1', '2' and '3' are presumed to consist of individuals resulting from spawning and settlement from 2020, 2019 and 2018, respectively. Individuals belonging to groups '1' and '2' were abundant at all three scrape sites in July while the larger group '3' were represented by single individuals at two of these sites (Fig. 2A). An additional cohort of smaller individuals less than a year old, the

Table 1. The relative abundance and relative biomass of quagga mussels to zebra mussels calculated from dredges on natural substrates in Lough Ree and Lough Derg. See details in the Suppl. material 2.

Area	Site	Date	Depth (m)	Relative abundance (%)	Relative biomass (%)
Lough Ree	R1	July '21	22.5	17.6	74.7
	R2	July '21	8.8–9.4	94.7	92.3
	R3	July '21	18	7.1	16.2
	R4	July '21	5.8–7.2	78.6	85.7
	R5	July '21	5–6	50.7	65.8
	R6	July '21	5.3	39.4	31.2
Lough Derg	D1	Sept '21	5.2	5.6	14.6
	D2	Sept '21	5.3	NA*	9.0
	D3	Sept '21	5.8	10.3	9.4
	D4	July '21	5.4	16.8	6.2
	D5	July '21	16	1.3	5.1

* Data not recorded.

Table 2. Population density of quagga mussels and zebra mussels calculated from scrapes on artificial surfaces within Lough Ree during summer 2021 and over winter 2021–2022.

Site	Date	Scrapes	Estimated individuals per m^2			Relative abundance (%)
			Quagga mussel	Zebra mussel	Dreissenids	Quagga mussel
Portrunny Harbour	July '21*	6	2173	1383	3556	61.1
	Jan '22	6	4817	2467	7284	66.1
Killinure Point	July '21*	5	4520	2308	6828	66.2
	Jan '22	4	20 233	6525	26 758	75.6
Hodson Bay	July '21*	3	4105	1970	6075	67.6
	Dec '21	5	15 612	2651	18 263	85.5

* Data from taken from Baars et al. (2022).

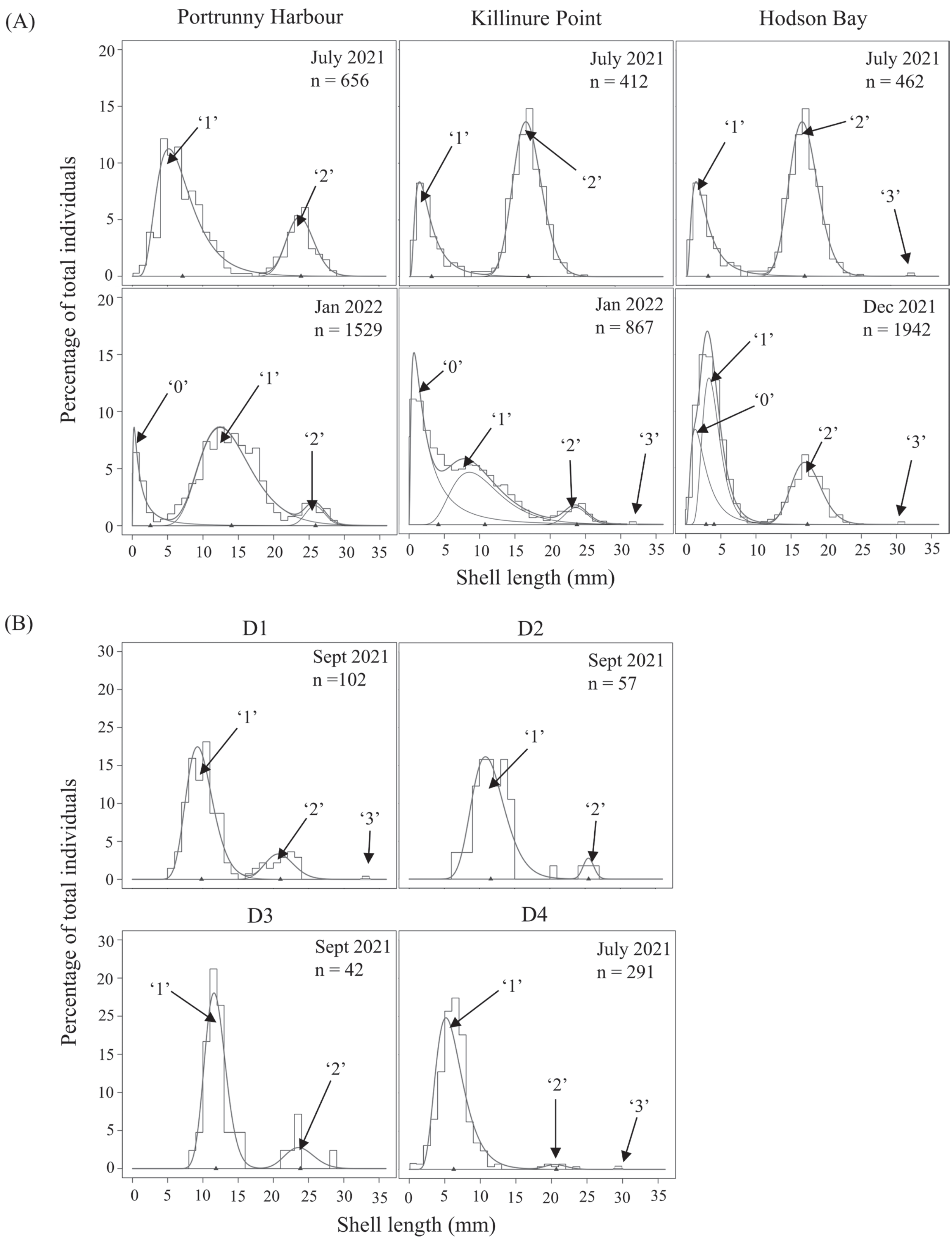

Figure 2. Mixture analysis applied to quagga mussel year cohorts which presumably spawned and settled in 2021 (group '0'), 2020 (group '1'), 2019 (group '2') and 2018 (group '3') in (**A**) scrape sites on artificial surfaces in Lough Ree in summer 2021 and winter 2021–2022 and (**B**) dredge sites on natural surfaces in Lough Derg in summer 2021. Group '3' was excluded from the analysis due to low numbers. Proportions for each cohort within the mixture analyses are reported in Table 3. The inside smoothed line represents component densities, obtained by fitting normal distributions to each cohort. The outer smoothed lines represent mixed densities, which were obtained by summing the component densities beneath it. These lines may overlap where year cohorts are distinct.

aforementioned young-of-the-year (group '0'), was detected within the December 2021 and January 2022 samples (Fig. 2A and Table 3).

Mean shell lengths for each year cohort varied between sites (Fig. 2A) and increased over time. The difference in mean shell length between group '1' and '2' within each sampling period was used to estimate growth on artificial surfaces and ranged from 11.9 to 16.8 mm per year (Table 4).

Table 3. Proportions (p̂) and standard errors (SE) of each year cohort of the quagga mussel taken from scrapes on artificial surfaces at sites Portrunny Harbour (PH), Killinure Point (KP) and Hodson Bay (HB) in Lough Ree and from dredges on natural substrates at sites D1–D4 in Lough Derg.

Area	Site	Goodness of fit (X^2)	Date	*n*	Modelled proportions (p̂ ± SE)		
					group '0'	group '1'	group '2'
Lough Ree	PR	<0.05	July '21	656		0.75 ± 0.02	0.25 ± 0.02
		<0.01	Jan '22	1529	0.15 ± 0.01	0.79 ± 0.02	0.06 ± 0.01
	KP	<0.05	July '21	412		0.76 ± 0.02	0.24 ± 0.02
		<0.01	Jan '22	867	0.52 ± 0.03	0.42 ± 0.03	0.06 ± 0.01
	HB	0.8	July '21	462		0.29 ± 0.02	0.71 ± 0.02
		<0.01	Dec '21	1942	0.27 ± 0.09	0.43 ± 0.09	0.3 ± 0.01
Lough Derg	D1	0.76	Sept '21	102		0.83 ± 0.03	0.17 ± 0.03
	D2	0.32	Sept '21	57		0.95 ± 0.03	0.05 ± 0.03
	D3	0.81	Sept '21	42		0.86 ± 0.05	0.14 ± 0.05
	D4	<0.01	July '21	291		0.98 ± 0.01	0.02 ± 0.01

Table 4. Estimations of yearly growth for quagga mussels based on the difference in mean shell lengths between cohorts (group '2' - group '1') identified by the R package Mixdist. Mussels at Portrunny Harbour (PH), Killinure Point (KP) and Hodson Bay (HB) in Lough Ree were sampled by scrapes on artificial surfaces while those at D1–D4 in Lough Derg were sampled by a dredge on natural substrates. Mean shell lengths for each cohort are shown in Fig. 2.

Area	Site	Date	n	Estimated growth (mm per year)
Lough Ree	PH	July '21	656	16.8
		Jan '22	1529	11.9
	KP	July '21	412	14.6
		Jan '22	867	13
	HB	July '21	462	14.2
		Jan '22	1942	13.6
Lough Derg	D1	Sept '21	102	11.2
	D2	Sept '21	57	13.9
	D3	Sept '21	42	12
	D4	July '21	291	14.4

Lough Derg

Quagga mussels were present on natural substrates at 47 of 159 locations occurring throughout the lake at depths of 2 to 32.5 m but with gaps in occurrence (Fig. 1). The relative abundance of quagga mussels to zebra mussels on natural substrates within LD ranged from 1.3 to 16.8% (Table 1). Similarly, relative biomass ranged from 5.1 to 14.6% on natural substrates in LD and was therefore much lower than in LR (Table 1). The shell length of 492 measured individuals ranged from 1 to 33 mm (Fig. 2B). Group '1' and '2' were present at all four measurement sites while group '3' was present at D1 and D4. The majority of individuals present were from group '1' with the relative proportion of group '1' to group '2' ranging from 0.83 to 0.98 (Table 3). Individuals on natural substrates were estimated to have a yearly growth rate of between 11.2 to 14.4 mm (Table 4).

Discussion

The quagga mussel is widely distributed within both lakes LR and LD at depths ranging from less than 1 to 32.5 m, colonising the firm and soft substrates common within these lakes. Quagga mussels were frequently attached to larger conspecifics, aquatic angiosperms and live individuals and empty shells of the zebra mussel and Asian clam *Corbicula fluminea* (Müller, 1774). Quagga mussels, zebra mussels and Asian clams were often found attached in clusters, providing each with a suitable substrate. Quagga mussels also utilised the empty shells of the native unionid duck mussel *Anodonta anatina* (Linnaeus, 1758) as a substrate for attachment. These native mussels, previously dominant in the shallows of both lakes, were extirpated during the zebra mussel invasion (Minchin 2014). The substrates utilised by the quagga mussel in the present study are similar to those which were utilised by the zebra mussel during its outbreak period in these lakes (Minchin et al. 2002; Minchin and Zaiko 2014; Zaiko et al. 2014).

The quagga mussel dominated the dreissenid community by abundance on all artificial surfaces sampled in LR (Table 2) and their abundance increased between summer and winter due to the presence of the young-of-the-year (Fig. 2A). Their prevalence was much less pronounced on natural substrates, with the quagga mussel dominating at 3 of 6 sites in LR and 0 of 5 sites in LD (Table 1). A lower relative abundance on natural substrates compared to artificial surfaces in LR could partially be due to two of the natural substrate sites being at depth (over 18 m). Ginn et al. (2018) indicates that the quagga mussel is slower to colonise areas in the profundal zone than shallower near shore sites. Therefore it is possible that the quagga mussel has not yet had enough time to colonize deeper substrates and that this may be expected in the near future. At present, quagga mussels only contributed 16.3% to total dreissenid abundance on natural substrates at their most prevalent site in LD. The expectation is that in LD quagga mussels will dominate over the next few years. An analysis of 13 sites in Germany and the Netherlands showed that the relative abundance of the quagga mussel increases at an average rate of 26% per year (Heiler et al. 2013). The relative abundance of quagga mussels in the Volga River increased from 4% in 1994, to 24% in 1995, to 32% in 1996, to 96% in 2000 (Orlova et al. 2004).

The presence of an additional mode between the summer and winter length-frequency distributions in LR establishes that each mode does in fact represent successive annual cohorts (Fig. 2A). The dominance of the most recently settled cohort at sites in both LR and LD (Table 3) suggests that high amounts of juvenile settlement is occurring, a characteristic of recently established quagga mussel populations (Mills et al. 1993; McMahon 2011). Some individuals of the 2018 year cohort (group '3') with a shell length of 30 to 34 mm, were present in LR and LD, although they were few in number (Baars et al. 2022). This study shows some decline in the abundance of the '1' group entering the following year that could indicate natural mortality and perhaps the small surviving number of individuals of group '3' will also have endured high mortality.

Clearly by 2021 the quagga mussel has become widespread in both lakes; but where the seminal introduction took place is unclear. The high densities within the sites of the inner lakes off the south-eastern region of LR is a possible locality, there being three marinas in this region. At Killinure Point densities of over 20 000 individuals per m^2 were obtained. The relative proportions and biomass of quagga mussels to zebra mussels on natural substrates are also high in this region (Table 1). Following the rationale of McMahon (2011), it is possible that the quagga mussel invaded the Shannon in 2017 in order for a sufficient number of adult individuals in 2018 to be produced capable of generating enough veligers to settle as individuals of the widespread 2019 cohort detected in our study.

We may also estimate a likely time of introduction of the quagga mussel using the linear regression y = 0.0721x-40 produced by Heiler et al. (2013), where y = the relative abundance (%) of quagga to zebra mussels and x = time (days) since initial introduction. Our highest recorded relative abundances of 85.5% on artificial surfaces (Hodson Bay Dec' 2021, Table 3) and 94.7% on natural substrates (R2 in July 2021, Table 1) provides an estimated time since introduction of 1740.6 and 1868.2 days. This translates to 4.7 to 5.1 years prior to July and December 2021, respectively, and provides evidence that the quagga mussel was introduced to Lough Ree sometime in 2016 or 2017. We have no indication of quagga mussel presence in 2016 in Hodson Bay and Portrunny Harbour within LR or at Dromineer and Rossmore in LD using the same sampling methods (unpublished data). Even so, the species may have persisted at abundances lower than monitoring would reasonably detect, similar to the sleeper populations proposed by Spear et al. (2021).

As with the zebra mussel, the most likely mode of introduction of the quagga mussel was as fouling on recreational vessels arriving from Britain or the European continent, having been transported by ferry (Pollux et al. 2003). Such craft are likely to have been launched at a marina site in LR during or before 2017. Given that zebra mussels took just four to five years to cause irreversible changes to the ecosystems of LR and LD (Zaiko et al. 2014), the quagga mussel is likely to already be having a large impact on the ecology of the lakes. Rising prevalence of quagga mussels and total dreissenid densities (Tables 1, 2) will only increase such impacts.

Our length-frequency distributions show that the growth of the quagga mussel is rapid, attaining sizes up to 34 mm. Larger shell sizes benefit dreissenid mussels by providing refuge from predation (Foley et al. 2017) and increasing reproductive output (Sprung 1991). The size ranges for groups '0', '1' and '2' are similar to those reported for quagga mussels in North America (Mills et al. 1993; McMahon 2011; Wong et al. 2012) and Europe (Imo et al. 2010; Aldridge et al. 2014; Balogh et al. 2018). Our maximum sized quagga mussel of 34 mm is similar to the 35 mm individuals in well-established lake populations in North America (Mills et al. 1999) and to the 32 mm individuals found in rivers in Eastern Europe (Imo et al. 2010), although larger than the 27 mm individuals reported from a lake in Hungary (Balogh et al. 2018) and a river in France (Bij de Vaate and Beisel 2011). While the quagga mussel's invasion of LR and LD is only recent, our study suggests that the lakes carry the largest reported individuals across their invasive range in Western Europe. This may be attributed to the lack of studies focusing on the population structure of the quagga mussel in large Western European lakes. However, such large body sizes may not be supported within LR and LD in future as the advantages of a lack of intraspecific competition (Metz et al. 2018) decline as overall densities increase within the lakes.

Estimated growth rates varied between 11.2 and 16.8 mm per year (Table 4) which may also be expressed as a range of 0.031 to 0.046 mm per day in order to allow for a comparison between studies of differing lengths. Our estimations are similar to the 0.031 mm per day growth rates reported for 15 m depths within Lake Ontario (Elgin et al. 2022) and the 0.04 mm per day growth rates from Lake Erie (MacIsaac 1994). Larger average growth rates of up to 0.08 mm per day were seen for newly settled mussels in natural populations in Lake Mead in South-Western USA (Wong et al. 2012). Even so, mussels of a similar age cohort to those within our study (~ 1 year old) showed growth rates of approximately 0.02 to 0.04 mm per day in Lake Mead (Wong et al. 2012). As our growth estimations rely on the distinguishability of cohorts, we based our assessment on the difference in size between group '1' and '2' as these were always distinct. At the sampling times, it was possible that further recruitment was still occurring and therefore mean size of group '0' was thought unreliable. By our winter sampling dates, cohorts became less distinguished (especially at Hodson Bay) as has been previously reported to happen as invasions progress (Nalepa et al. 1995). From a comparison between the summer and winter sampling dates for each site, the size difference between group 1 and 2 decreases, suggesting that group ‘1’ grows more rapidly than group ‘2’ which would be expected - Wong et al. (2012) reports that smaller quagga mussels grew more rapidly.

The present study suggests that growth rates varied between sites within LR (Table 4). For example, the mean shell length of each year cohort in Hodson Bay was much lower than the corresponding cohort in Portrunny Harbour or Killinure Point (Fig. 2). The factors contributing to these spatial differences in mean shell length of cohorts and estimated growth rates require further study and may be either environmental or due to intra- and interspecific competition as demonstrated by Metz et al. (2018). The quagga mussel at Hodson Bay was still highly dominant despite lower mean sizes and estimated growth rates showing that invasion success was still maintained under less suitable conditions.

Conclusion

The arrival of the quagga mussel to Lough Ree and Lough Derg probably took place in 2016 or 2017. Its high densities and dominance over zebra mussels in LR would suggest that this is where it first arrived, most likely on trailered vessels from Britain or Europe, after which it dispersed downstream by natural water currents and perhaps by fouling the hulls of cruising craft. The quagga mussel’s successful colonisation of the lakes is in part due to the availability of shell surfaces of native and invasive mussels, which provide a widespread substrate for attachment especially over soft sediments. The quagga mussel is likely to continue to expand its range within the Shannon navigation and enter other river catchments through linking canals with hull transport and overland with trailered craft. Our study shows that the quagga mussel was undetected for a long period of time, suggesting that species on horizon lists require specific surveillance monitoring. Early detection could help target interventions that may reduce the spread of these non-native species or allow for their eradication where feasible.

Its widespread distribution and high abundance in these two large lakes, together with its historic developments in lakes elsewhere, would indicate that the quagga mussel is likely to, if it does not already, impact freshwater biodiversity and human activities within the River Shannon system.

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Author Contributions

OF: Research conceptualization, sample design and methodology, investigation and data collection, data analysis and interpretation, writing – original draft. DM: Sample design and methodology, investigation and data collection, data analysis and interpretation, writing – review & editing. MBC: Investigation and data collection, writing – review & editing. KOL: Investigation and data collection, writing – review & editing. HS: Investigation and data collection, writing – review

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Supplementary material 1

Georeferenced sampling sites including quagga mussel records for Lough Ree and Lough Derg

Authors: Oscar Flynn, Dan Minchin, Martina B. Caplice, Kate O'Leary, Heather Swanwick, Jan-Robert Baars

Data type: xlsx

Link: https://doi.org/10.3391/ai.2023.18.4.111650.suppl1

Supplementary material 2

Abundance and biomass of quagga and zebra mussels in dredge samples R1–R6 and D1–D5

Authors: Oscar Flynn, Dan Minchin, Martina B. Caplice, Kate O'Leary, Heather Swanwick, Jan-Robert Baars

Data type: xlsx

Link: https://doi.org/10.3391/ai.2023.18.4.111650.suppl2